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Abstract: Angiosperms and their flowers have greatly diversified into an overwhelming array of forms in the past 135 million years. Diversification was shaped by changes in climate and the biological environment (vegetation, interaction with other organisms) and by internal structural constraints and potentials. This review focuses on the development and structural diversity of flowers and structural constraints. It traces floral diversification in the different organs and organ complexes (perianth, androecium, gynoecium) through the major clades of extant angiosperms. The continuously improved results of molecular phylogenetics provide the framework for this endeavor, which is necessary for the understanding of the biology of the angiosperms and their flowers. Diversification appears to work with innovations and modifications of form. Many structural innovations originated in several clades and in special cases could become key innovations, which likely were hot spots of diversification. Synorganization between organs was an important process to reach new structural levels, from which new diversifications originated. Complexity of synorganization reached peaks in Orchidaceae and Apocynaceae with the independent evolution of pollinaria. Such a review throughout the major clades of angiosperms also shows how superficial and fragmentary our knowledge on floral structure in many clades is. Fresh studies and a multidisciplinary approach are needed.

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EVOLUTIONARY DIVERSIFICATION OF THE FLOWERS IN ANGIOSPERMS[1]

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Angiosperms and their flowers have greatly diversified into an overwhelming array of forms in the past 135 million years. Diversification was shaped by changes in climate and the biological environment (vegetation, interaction with other organisms) and by internal structural constraints and potentials. This review focuses on the development and structural diversity of flowers and structural constraints. It traces floral diversification in the different organs and organ complexes (perianth, androecium, gynoecium) through the major clades of extant angiosperms. The continuously improved results of molecular phylogenetics provide the framework for this endeavor, which is necessary for the understanding of the biology of the angiosperms and their flowers. Diversification appears to work with innovations and modifications of form. Many structural innovations originated in several clades and in special cases could become key innovations, which likely were hot spots of diversification. Synorganization between organs was an important process to reach new structural levels, from which new diversifications originated. Complexity of synorganization reached peaks in Orchidaceae and Apocynaceae with the independent evolution of pollinaria. Such a review throughout the major clades of angiosperms also shows how superficial and fragmentary our knowledge on floral structure in many clades is. Fresh studies and a multidisciplinary approach are needed.

Key words: angiosperms; ANITA grade; diversification; eudicots; floral evolution; floral structure; innovation; magnoliids; monocots.

Our perception of flower evolution in angiosperms has greatly changed over the past 20 years following the revolution of angiosperm phylogenetics, especially since the seminal large-scale work on molecular phylogenetics through the major groups of seed plants by Chase et al. (1993). The recovery of many well-preserved floral fossils from the Cretaceous when angiosperms began to diversify greatly contributed to better knowledge of historical depth in flower evolution (Crane et al., 1995; Friis et al., 2006; Magallón and Castillo, 2009). The introduction of evolutionary aspects to molecular developmental studies of flowers added yet another facet to the field (e.g., Irish, 2009; Kramer, 2009; Soltis et al., 2009; Specht and Bartlett, 2009; Theissen, 2009). From the phylogenetic studies at different levels of the systematic hierarchy, we have a more detailed (yet still very incomplete) idea about evolutionary changes of floral features. It can be more clearly seen how evolutionary directions of changes, also of putatively conservative characters, are much more flexible than previously thought (e.g., Endress and Doyle, 2009; Saunders, 2010; Endress, in press).

Angiosperms as currently perceived are represented by several major clades, the basal angiosperms with the clades forming the ANITA grade (Amborellaceae, Nymphaeales, Austrobaileyales, and, perhaps, Chloranthaceae plus Ceratophyllaceae), and magnoliids, and the two especially species-rich clades monocots and eudicots (Qiu et al., 1999; Stevens, 2001 onward; Judd and Olmstead, 2004; Soltis et al., 2004, 2005; Angiosperm Phylogeny Group, 2009; for Chloranthaceae and Ceratophyllaceae, see also Doyle and Endress, 2000; Qiu et al., 2010) (Fig. 1). Many of the major subclades (orders and groups of orders) have new circumscriptions as compared to those in premolecular works (e.g., Cronquist, 1981) and need therefore to be characterized in their structure and biology (Bremer et al., 2001; Endress and Matthews, 2006b; Schönenberger et al., 2010), but knowledge of the longer established clades also needs to be improved. Even completely new larger clades, such as Crossosomatales (Sosa and Chase, 2003) and Huerteales (Worberg et al., 2009), appeared.

A survey of flower evolution and evolutionary trends in a large group can be organized in different ways. One way is to treat each major clade, as was done for the major subclades of eudicots (Endress, 2010a), another way is to follow salient features through the entire clade under review. Thus the focus can be on either clades or features. The second way, to focus on features, is followed here for the entire angiosperms. The basis for this endeavor is a database compiled from over 3300 original publications for core eudicots and monocots. In addition, the published results on the gynoecia of the basalmost angiosperms, magnoliids, basal monocots, and basal eudicots of our laboratory were used, which all contain extensive original data and reviews of the literature available at the time (Endress and Igersheim, 1997, 1999, 2000a, b; Igersheim and Endress, 1997, 1998; Endress et al., 2000; Igersheim et al., 2001). Also the comparative studies on several orders of rosids in our laboratory resulted in a broad database (Matthews et al., 2001; Matthews and Endress, 2002, 2004, 2005a, b, 2006, 2008; Endress and Matthews 2006b; Bachelier and Endress, 2007, 2008, 2009; see also Endress and Friis, 2006; Schönenberger and von Balthazar, 2006). The attempt to consider all larger clades of angiosperms has the advantage of elucidating convergent features in various groups that may help us to better understand or to put into perspective evolutionary trends in one group from evidence in another.

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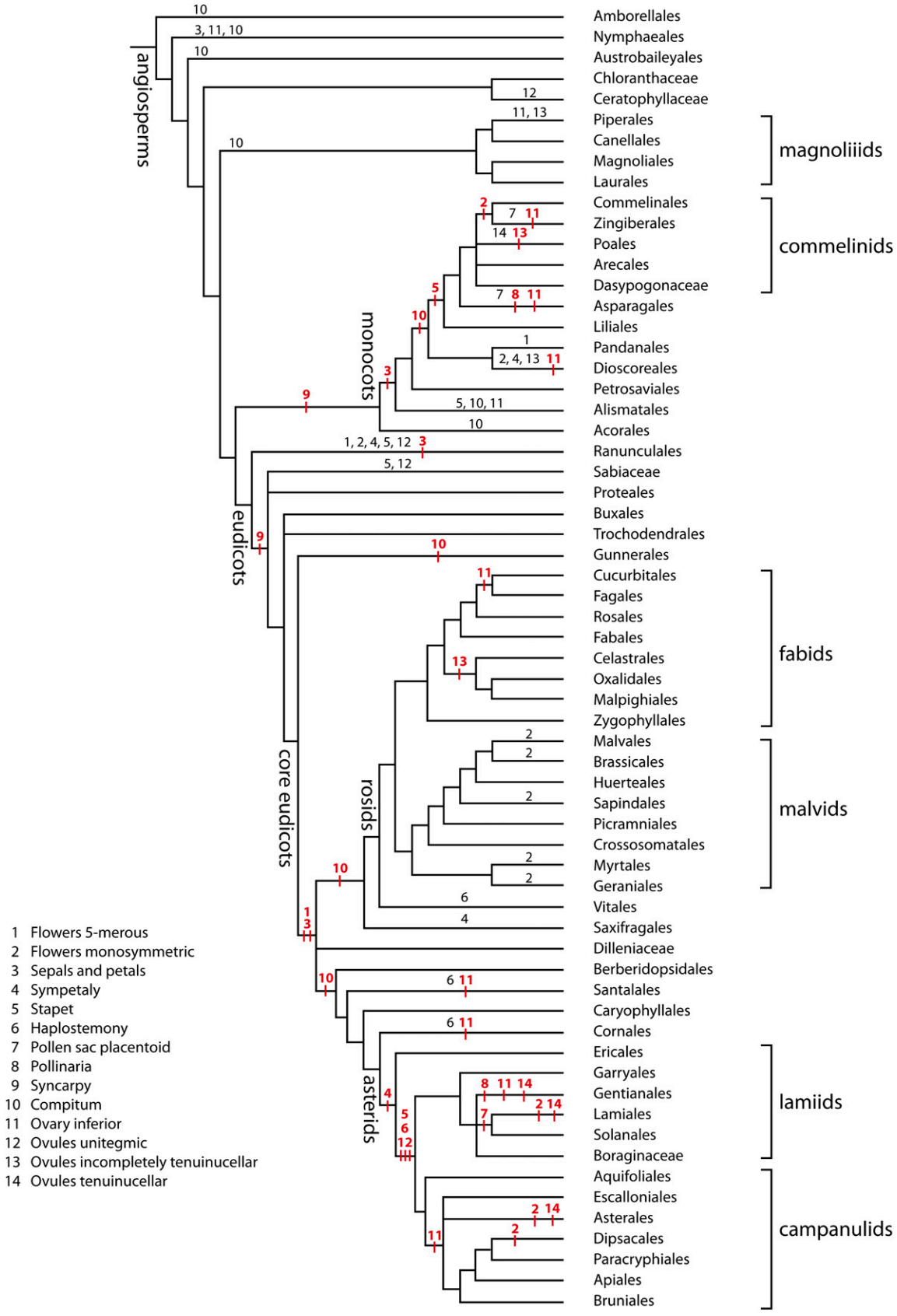

Fig. 1. Cladogram of angiosperms (modified after Angiosperm Phylogeny Group, 2009). Potential key innovations of indicated clades or parts of them in red and marked with a line on the branch. Nonkey innovations black and not marked with a line. (Stapet: organ complex of stamen fused with perianth organ)

SOME PRICIPLES OF DIVERSIFICATION AND STABILITY

Evolutionary changes leading to diversification are shaped by morphogenetic and architectural possibilities and limitations and by functional and ecological constraints. Thus openness for directions of diversification is limited by stabilizing "forces". Some changes are easier to achieve than others, and this proneness for changes may differ from group to group. There is pervasive convergence. Repeated evolution of similar features is much more common than was believed earlier (Endress, in press). We can recognize a family from a quick glance at a flower in many cases. However, it also happens that we are blinded by convergence and are led down a wrong track.

Two contrasting principles of evolution are (1) progressive elaboration (especially by synorganization and fixation at certain structural levels and opening of flexibility at new structural levels and (2) simplification by reduction, and loss of fixation, "reversals" (Endress, 1994a, 2001c, 2006, 2010a). Highly elaborated and synorganized flowers will be found especially in "highly nested" groups of angiosperms, groups that have experienced many rounds of adaptive radiations based on key innovations. In some basal angiosperms, relatively highly elaborate flowers are also present but based on different innovations, in general with less intricate synorganization of parts. An important aspect of elaboration is economization of structures, which can be followed especially in the androecium and gynoecium in various ways.

As our knowledge of phylogenetic relationships of angiosperms at all systematic levels is continuously improving, progressive elaboration of floral features can be perceived with increasing clarity. It can be plotted on a phylogenetic tree, where a feature appears for the first time (Fig. 1). Such innovations may have different macroevolutionary significance. Either they have no noticeable evolutionary effect or they may trigger an adaptive radiation and then represent key innovations. Innovations may not be conspicuous at first but eventually become key innovations when the right conditions (ecological, genetic structure) are present (examples in Endress, 2010a).

The focus of this paper is on some salient features and evolutionary trends throughout the angiosperms, mainly from a comparative morphological and developmental perspective, in contrast to many works that focus on ecological aspects in smaller groups of angiosperms.

FLORAL PHYLLOTAXIS

Phyllotaxis of floral organs (in short: floral phyllotaxis) is measured in divergence angles (the angle between two subsequently initiated organs with the floral center). The time from the initiation of one organ to the initiation of the subsequent organ is called a plastochron. Floral phyllotaxis is either spiral, whorled, complex-whorled, or irregular. In spiral phyllotaxis, the subsequent organs have equal divergence angles and equal plastochrons. In flowers with spiral phyllotaxis, the mean divergence angles are almost always 137.5° (Fibonacci pattern). In whorled phyllotaxis, the organs within one whorl have equal divergence angles, but the divergence angle from the last organ of a whorl to the first organ of the subsequent whorl is different; likewise, the organs within each whorl have very short plastochrons (tending to zero), but the plastochron between the last organ of a whorl and the first organ of the subsequent whorl is long (see Endress, 1987a). From this, it follows that organs originate in spiral sequence not only in spiral phyllotaxis but often also in whorled phyllotaxis (e.g., Erbar and Leins, 1985, 1988, 1997; Leins and Erbar, 2004; Schönenberger and Grenhagen, 2005). Unfortunately, this spiral sequence has often been confused with spiral phyllotaxis in the literature. In a given flower, all whorls have the same number of organs, and as a rule, there is alternation of the organs from whorl to whorl (Fig. 2A, C). In the complex-whorled pattern, however, the organ number changes from whorl to whorl. Where an organ is expected, there are two collateral organs (double position) or more than two (multiple position) (Fig. 2B) (e.g., Staedler and Endress, 2009). From the periphery to the center of a flower organ, the number per whorl often first increases and then decreases again in this pattern. In irregular phyllotaxis, there is no apparent pattern in organ position. In spiral phyllotaxis, organs of the same category tend to occur in series of Fibonacci numbers because each time a Fibonacci number is reached in the course of floral development, the arrangement of organs has a higher degree of regularity than for other numbers (see Hirmer, 1931; Endress, 1987a; Staedler et al., 2007). Thus, series in spiral systems are in some way comparable to whorls in whorled systems.

Floral phyllotaxis can be best recognized in young floral buds when the organs have not yet elongated. All regular phyllotaxis patterns show floral organs aligned in spiral lines (parastichies). Sets of parastichies go in both directions. In spiral phyllotaxis, the parastichies of different directions have different steepness. In contrast, in whorled phyllotaxis, they have the same steepness. In addition, in whorled phyllotaxis, but not in spiral phyllotaxis, the organs are also aligned in radial lines (orthostichies) (Endress, 2006).

In basal angiosperms, spiral floral phyllotaxis occurs along with whorled phyllotaxis and is present in some members of the ANITA grade (e.g., Amborellaceae, Endress and Igersheim, 2000b; Austrobaileyales, Endress, 1980b, 2001b; Endress and Sampson, 1983) and magnoliids (e.g., Erbar and Leins, 1981; Endress 1986b). In contrast, spiral floral phyllotaxis is absent in monocots, and most core eudicots (even in flowers with free carpels, such as Alismatales, e.g., Leins and Stadler, 1973; Sattler and Singh, 1978; or Rosaceae, Lindenhofer and Weber, 2000; in both Alismatales and Rosaceae, stamens and carpels are in complex whorls with double or multiple organ positions). In core eudicots with 5-merous flowers, although the two prophylls and the outer sepals may begin as a system with spiral phyllotaxis, the inner sepals or the petals change to whorled. The outer organs that are positioned in a spiral phyllotaxis are initiated with relatively long plastochrons, but the shorter the plastochrons become, the more the phyllotaxis tends to become whorled. Only rarely do inner perianth parts also have long plastochrons, and then the transition from spiral to whorled phyllotaxis is delayed. Such delay occurs sporadically in the core eudicots such as in Paeoniaceae (*Paeonia*, Hiepko, 1965a), Dilleniaceae (*Dillenia*, Endress, 1997), Sapindaceae (*Averrhoidium*, Weckerle and Rutishauser, 2003), Cactaceae (*Pereskia*, Leins and Schwitalla, 1985), Phytolaccaceae (*Phytolacca*, Ronse Decraene et al., 1997, clearly seen in their fig. 3B, although they interpret the pattern differently), Theaceae (*Stewartia*, Erbar, 1986; *Hartia*, Tsou, 1998). In some of these taxa (Paeoniaceae, Cactaceae, some Theaceae), the number of perianth parts is increased, and there are numerous stamens, which are initiated in groups. These stamen groups either continue the spiral phyllotaxis (Paeoniaceae, Hiepko, 1965a; Cactaceae, Leins and Schwitalla,

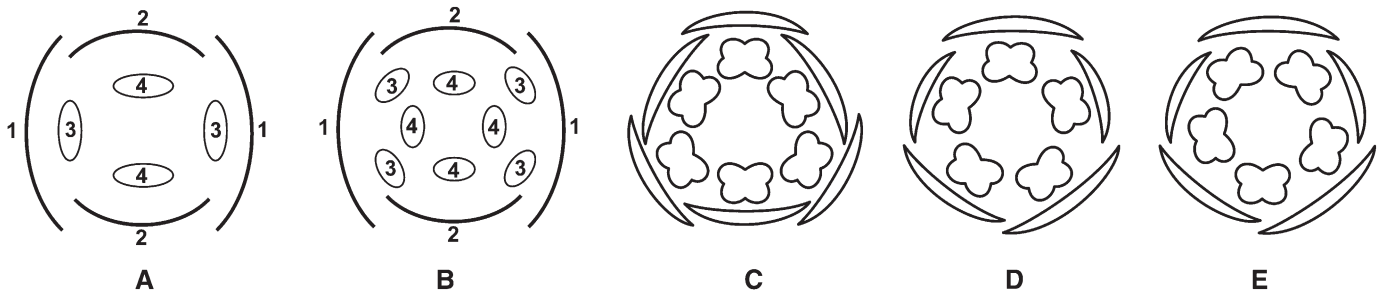

Fig. 2. (A, B) Whorled phyllotaxis patterns. (A) Simple whorled (2-merous). (B) Complex whorled with change from 2-merous to 4-merous by double organ positions in the third whorl. (C–E) Floral merism. (C) 3-mery: 4 alternating whorls (2 perianth whorls, aestivation open in each whorl, 2 stamen whorls). (D, E) 5-mery: 2 whorls (1 perianth whorl, aestivation quincuncial, 1 stamen whorl). (D) Stamen whorl opposite perianth organ whorl. (E) Whorls alternating.

1985), or they are positioned in the radii of the innermost perianth parts (some Theaceae, Erbar, 1986; Tsou, 1998). Irregular phyllotaxis is common in flowers with numerous floral organs, especially flowers with numerous stamens. It is present in some taxa in most major clades of angiosperms, among basal angiosperms, (e.g., in the most extremely polystemonous Nymphaeales [Endress, 2001b] and Magnoliales [Zagórska-Marek, 1994; Endress, 2006]; among monocots in Arecales [Uhl and Dransfield, 1984]; among basal eudicots in Ranunculales [Ren et al., 2010]; and among core eucots in fabids [Gemmeke, 1982] and malvids [Leins and Metzenauer, 1979; Janka et al., 2008]). Irregular phyllotaxis of stamens is present in flowers in which stamens develop from secondary primordia formed on primary primordia, especially when the initiation pattern is centrifugal (e.g., Capparaceae [Leins and Metzenauer, 1979; Karrer, 1991]; Dilleniaceae, *Dillenia* [Endress, 1997]; Lecythidaceae [Endress, 1994a]).

Complex whorls are common in many larger groups of angiosperms. The site with the first double positions in a flower is not always the same; it is usually somewhere in the perianth or the androecium, commonly when there is a switch from broader to more narrow organs. Double positions occur especially in basal angiosperms, basal monocots, and basal eudicots. In basal angiosperms, they are known from Nymphaeales (Cabombaceae [androecium], Nymphaeaceae [perianth], Endress, 2001b), Magnoliales (Annonaceae [androecium], Endress, 1987a; Leins and Erbar, 1996), Laurales (Atherospermataceae, Monimiaceae [perianth or androecium], Staedler and Endress, 2009; Lauraceae [androecium], Endress, 1987a), Canellales (Winteraceae, *Takhtajania* [perianth], Endress et al., 2000; Canellaceae [androecium], Wilson, 1966), and Piperales (Aristolochiaceae, *Saruma* [androecium], Leins and Erbar, 1995). In monocots, they occur in Alismatales (androecium) (Erbar and Leins, 1994) and Cyclanthaceae of Pandanales (gynoecium) (Rudall and Bateman, 2006). In basal eudicots, they characterize Papaveraceae, e.g., *Eschscholzia* (androecium) (Endress, 1987a); Berberidaceae, *Podophyllum*, (androecium) (deMaggio and Wilson, 1986; Ronse De Craene, 2010); Ranunculaceae (androecium) (Schöffel, 1932); Buxaceae (androecium) (von Balthazar and Endress, 2002a, b); and *Tetracentron* (gynoecium) (Endress, 1986a; Chen et al., 2007). In core eudicots, they have a scattered occurrence (Ronse Decraene and Smets, 1993a, b, 1996, 1998). Examples are Brassicaceae and Cleomaceae (perianth and androecium) (Endress, 1992), Apodanthaceae (perianth) (Blarer et al., 2004) or Fouquieriaceae (androecium) (Schönenberger, 2009).

In sum, in basal angiosperms and basal eudicots, whorled and spiral floral phyllotaxis coexist sometimes at low systematic levels and may change during evolution to the other pattern relatively easily (Endress, 1987a, 2001b, 2006; Ronse De Craene et al., 2003; Endress and Doyle, 2007; Staedler and Endress, 2009). Thus, it is currently uncertain whether spiral or whorled floral phyllotaxis is ancestral in basal angiosperms; it appears however, that whorled phyllotaxis is ancestral in Magnoliales and eudicots, and not spiral as earlier believed (Endress and Doyle, 2007, 2009). In contrast, in more derived groups with a higher degree of synorganization between floral organs, there is a strong constraint to whorled phyllotaxis, as in monocots whorled floral phyllotaxis is exclusively present, and in core eudicots, almost so (Leins and Stadler, 1973; Sattler and Singh, 1978; Endress, 1987a, 2006).

FLORAL SYMMETRY

Angiosperms are characterized by multiple evolution of floral monosymmetry (with a single symmetry plane) and asymmetry (without a symmetry plane) (Donoghue et al., 1998; Endress, 1999, 2001a; Rudall and Bateman, 2002, 2004; Marazzi et al., 2006; Marazzi and Endress, 2008). Monosymmetry is a trigger for diversification because of precise positioning of pollinators on the flower, and consequently, more efficient pollination and enhanced pollinator specificity (Sargent 2004). This is even more accentuated for asymmetry, if derived from monosymmetry (Jesson and Barrett, 2003). Floral symmetry is a special focus of evo-devo studies (Cubas, 2004; Howarth and Donoghue, 2005, 2006; Busch and Zachgo, 2009; Jabbour et al., 2009; Mondragón-Palomino and Theissen, 2009; Preston and Hileman, 2009). Floral monosymmetry can be expressed in early floral development or just before anthesis, which may reflect differential depth of rooting in the genetic system and different evolutionary age. This structure of the genetic system needs more detailed study.

FLORAL MERISM

Merism relates to the number of floral organs in a whorl or series (Ronse Decraene and Smets, 1994). In many flowers, the merism is constant through all whorls. However, it may change in inner whorls, especially in the androecium and gynoecium. In complex whorls, the merism changes (see Floral phyllotaxis).

The predominance of trimerous flowers in monocots and pentamerous flowers in core eudicots is well known. This difference in merism has some impact on the behavior of the perianth. If the perianth has two whorls, it consists of six organs in monocots and of 10 in eudicots. In some way, the presence of two trimerous whorls (six organs) (Fig. 2C) is more similar to the presence of one pentamerous whorl (five organs) (Fig. 2D) instead of two whorls (10 organs). This similarity is also expressed in the predominant aestivation pattern of the organs. In the case of six organs, the three outer organs cover the three inner organs (Fig. 2C), and in the case of five organs, they cover each other in a quincuncial pattern (see Perianth aestivation) (Fig. 2D). Such evolutionary fluctuation from pentamery to trimery and back to pentamery can be followed in the sepals of Polygonaceae (Frye and Kron, 2003). The predominance of the numbers three and five (and not four) may be because three and five are Fibonacci numbers. If floral organs are initiated in a spiral sequence, the outermost organs may also have a (transitional) spiral phyllotaxis and thus tend to establish whorls in Fibonacci numbers (Endress, 1987a). However, this needs more detailed studies. The more rare cases of tetramerous perianth (or calyx) may be derived from two dimerous whorls (and those, in turn, from two trimerous whorls, with loss of an organ per whorl) or from a pentamerous condition by loss of one organ, depending on the systematic position. The first may be the case, e.g., in some basal eudicots (Proteaceae) or monocots (Stemonaceae), the second in some Lamiales (Oleaceae).

In contrast to the dominance of trimery in monocots and pentamery in core eudicots, merism is more flexible in basal angiosperms and basal eudicots. Among basal angiosperms trimery is not uncommon in whorled flowers, such as in Cabombaceae (ANITA grade); Magnoliaceae (Magnoliales); Lauraceae (Laurales); and Aristolochiaceae, Piperaceae, and Hydnoraceae (Piperales); whereas pentamery is rare and is present in Canellaceae (Canellales). In flowers with spiral phyllotaxis, the merism of the series commonly fluctuates within a flower along various Fibonacci numbers, such as in Calycanthaceae (Laurales) (Staedler et al., 2007) and Ranunculaceae (Schöffel, 1932). In basal eudicots, dimerous and trimerous flowers are dominant (Drinnan et al., 1994; von Balthazar and Endress, 2002a, b; Rutishauser et al., 2004; Ronse De Craene and Wanntorp, 2006; Chen et al., 2007; González and Bello, 2009; von Balthazar and Schönenberger, 2009; Endress, 2010a), whereas pentamerous flowers are rare and largely restricted to some Ranunculaceae (Ranunculales) and Sabiaceae (Endress, 2010a).

PERIANTH

Flexibility in developmental patterns of petals—Commonly, the organs of the outer perianth whorl, the sepals, are the protective organs in floral bud, whereas those of the inner whorl, the petals, are optically attractive in the open flowers. There are, however, a vast diversity of forms in sepals and petals and many exceptions from these functions (Endress and Matthews, 2006a; Ronse De Craene, 2008; Endress, 2010a). In eudicots (Hiepko, 1965b) and some monocots (e.g., Alismatales, Leins and Stadler, 1973) petals may be delayed in development after initiation. Their main growth begins only shortly before anthesis (Fig. 3A). Thus, they use not much space in bud, and buds stay relatively small. This behavior is commonly not present in the ANITA grade and magnoliids, in which the perianth organs are structurally less different from each other, although they may have the same differentiation in function as eudicots. For this reason, the outer and inner organs in the ANITA grade and magnoliids have often been uniformly called tepals (and not sepals and petals). A lower degree of differentiation in these groups is also found in molecular developmental aspects (Soltis et al., 2009). However, a delay of the inner whorl was observed in *Cabomba* (Cabombaceae) (Endress, 2001b, 2002), and in *Nuphar* (Nymphaeaceae) and *Saruma* (Piperales) there is also strong structural differentiation (e.g., Endress, 2008a). A delay of the petals is pronounced in basal eudicots (Ranunculales, Hiepko, 1965b; Merxmüller and Leins, 1967; Karrer, 1991; Endress, 2005b, 2010a), and especially in core eudicots. However, not all core eudicots show this pattern. In many clades, the organs of the second perianth whorl (petals) have become the main protective organs in bud (Fig. 3B): in rosids (e.g., Vitales [Gerrath and Posluszny, 1988]; Myrtales [Schönenberger and Conti, 2003]; Sapindales [Ronse De Craene and Haston, 2006; Bachelier and Endress, 2009]; Celastrales [Matthews and Endress, 2005a]; Crossosomatales [Matthews and Endress, 2005b]), as well as in

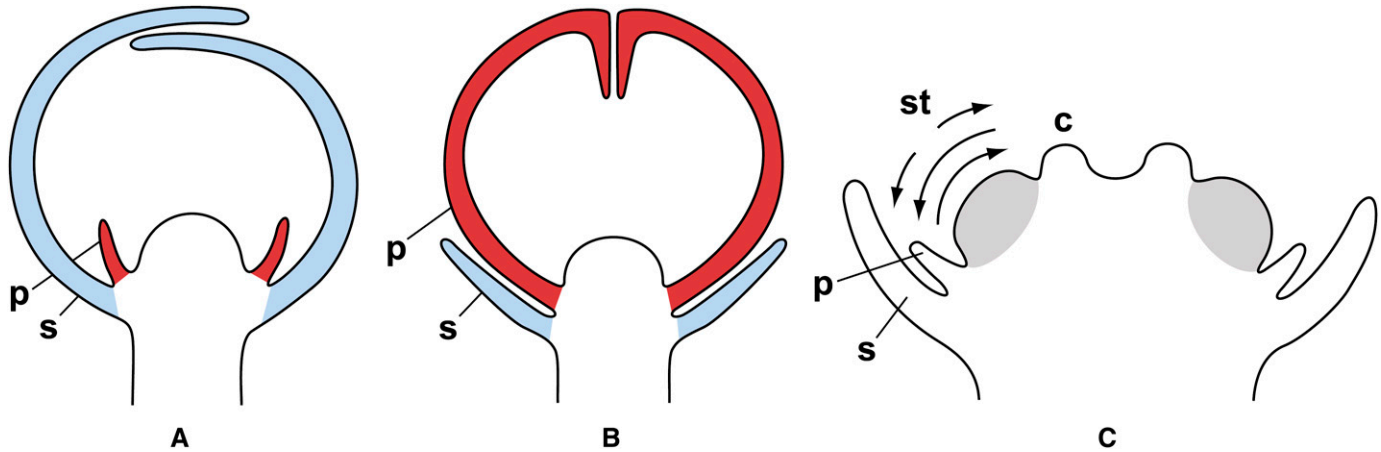

Fig. 3. (A, B) Floral buds with different perianth differentiation. Longitudinal sections. (A) Sepals (blue) large, imbricate, function as protective organs; petals (red) delayed after initiation. (B) Sepals (blue) remaining small; petals (red) large, valvate, function as protective organs. (C) Bud of polystemonous flower with primary androecium primordium (shaded gray) and possible directions of initiation of secondary primordia (stamens) indicated by arrows. Schematic longitudinal section. c, carpel; p, petal; s, sepal; st, androecium.

the asterid alliance (e.g., Santalales [Endress, 1994a; Eberwein et al., 2009; Wanntorp and Ronse De Craene, 2009], Cornales [Hufford, 1997a; Endress, 2010a], Rubiaceae [Vaes et al., 2006; Endress, 2010a], and many campanulids [Leins and Erbar, 1987; Gustafsson and Bremer, 1995; Endress, 2010a]). In many monocots, the differentiation between sepals and petals is less conspicuous than in eudicots, and often the organs of both whorls function in bud protection (Weber, 1980). Monocot groups with strong differentiation and the petals not involved in bud protection are some Alismatales, Commelinales, and Zingiberales. From the distribution of the absence and presence of petals, it appears that petals evolved or disappeared and re-evolved many times in angiosperms (e.g., Caryophyllales, Brockington et al., 2009).

Molecular developmental studies have especially focused on the development of the perianth in model species, but are expanding to include other taxa to better understand evolutionary aspects (e.g., Hileman and Irish, 2009; Irish, 2009; Kramer, 2009; Kramer and Hodges, 2010; Rasmussen et al., 2009; Soltis et al., 2009; Theissen, 2009; Bartlett and Specht, 2010). A more intimate collaboration between the two fields of diversity research and molecular developmental genetics should be promising.

Perianth aestivation and organ fusion within and between whorls—Aestivation designates the mutual positions of organs of a whorl in bud. They may overlap with their neighbors (imbricate aestivation) or be contiguous without overlapping (valvate aestivation) or be apart from them (open aestivation). Patterns of imbricate aestivation in whorls of five organs are quincuncial (two outer organs, two inner organs, and one organ with an outer and an inner flank), or cochlear (one outer organ, one inner organ, and three organs each with an outer and an inner flank), or contort (all five organs each with an outer and an inner flank). Valvate aestivation can develop from a basically quincuncial pattern by mainly thickening instead of further broadening of organs (e.g., *Delonix*, Fabaceae, Endress, 1994a). Some of the properties of the inner whorl or series of perianth organs, such as thickness, coloration, and hairiness, are directly dependent on physical interactions with the outer whorl. Thus, organ parts that are covered by other parts may attain different properties than parts that are not covered (Rohweder, 1970; Endress, 2008b; Warner et al., 2009). This needs more comparative and experimental study.

If five sepals (tepals) are present—a common situation in eudicots—they are mostly quincuncial (Fig. 2D, E). This is also true for the rare pentamerous monocots, such as *Pentastemona* (Stemonaceae, van Heel, 1992; Fukuhara et al., 2003) and for *Sparganium* (Typhaceae), which often has five sepals (Müller-Doblies, 1969). This quincuncial aestivation reflects the spiral initiation sequence of the organs. In contrast, petals are often contort or irregular, which reflects the much shorter plastochrons or the late expansion of petals compared with those of the sepals or tepals (Endress, 2005b, 2006). Contort petal aestivation is especially common in the large malvid clade of rosids (Endress and Matthews, 2006b) and also in Gentianales (asterids, Endress, 2010a). In strongly monosymmetric flowers, such as in Lamiales, sepals and petals are often cochlear, which reflects the unidirectional appearance of organs along the symmetry plane, which is superimposed onto the spiral sequence (Endress, 1999). Valvate aestivation, if present, occurs preferentially in the whorl that is protective in bud, thus more often in sepals than in petals (see above). It is not uncommon in eudicots, but more rare in monocots (e.g., Hypoxidaceae [sepals], Correll and Correll, 1982; Triuridaceae [sepals or both sepals and petals], Rudall, 2008; some Arecaceae [*Cocos nucifera*: petals], Correll and Correll, 1982).

In monocots, the six organs of the two perianth whorls are in general more coordinated than the 10 organs in eudicots. All six organs of the two whorls have more often similar properties, and if they are fused, all six organs often form a single unit. There is, however, also flexibility in this trait. For instance, in Arecaceae, the outer whorl may be fused (e.g., *Pseudophoenix*), or the inner whorl (e.g., *Roystonea hispaniolana*), or both whorls are fused into one tube (e.g., *Coccothrinax*), Correll and Correll, 1982). In eudicots, the two whorls behave much more independently with regard to histology and fusion.

Perianth elaboration and reduction—Perianth elaboration and synorganization went in diverse directions in angiosperms and are in general tightly linked to the entire architecture of the flower, often also including fusion with stamens (Endress and Matthews, 2006a) (see Synorganization between perianth and androecium). It reaches peaks in clades with highly monosymmetric flowers, such as in Burmanniaceae and Orchidaceae among monocots (Vogel, 1959), and in Fabales (Fabaceae, Polygalaceae) and Lamiales among core eudicots (Endress, 1994a; Westerkamp and Weber, 1999; Prenner, 2004; Westerkamp and Classen-Bockhoff, 2007; Bello et al., 2010).

Whereas loss of petals occurred numerous times in flower evolution and may even characterize large clades (e.g., part of Cyperaceae, Fagales), strong reduction or loss of only the sepals is less common. It occurs in some clades in which the protective function of floral buds was transferred to the petals (e.g., Apiaceae, Araliaceae, and Rubiaceae, Endress 2010a; Nuraliev et al., 2010) or to the enlarged floral prophylls (e.g., Acanthaceae-Thunbergioideae, Schönenberger and Endress, 1998; Schönenberger, 1999; Borg et al., 2008).

Reduction or loss of the entire perianth also occurs and is more common in clades with a low level of elaboration and synorganization, thus more in basal groups. Floral bud protection is then commonly exerted by floral subtending bracts, floral prophylls, or other organs adjacent to the flowers. In the ANITA grade, perianthless flowers evolved in Hydatellaceae (Hamann, 1975; Rudall et al., 2007), Chloranthaceae (except for female *Hedyosmum*) (Endress, 1987b; von Balthazar and Endress, 1999), and perhaps Ceratophyllaceae (Endress, 2004); among magnoliids in Piperales (Tucker et al., 1993), Eupomatiaceae, and perhaps Himantandraceae (Magnoliales) (Endress, 1977, 2003a; Kim et al., 2005), and some Lauraceae (*Lindera, Litsea*) (Laurales) (Endress, 1990); in basal monocots in some Araceae and other Alismatales (Buzgo, 2001; Barabé and Lacroix, 2008); in higher monocots in Pandanaceae (Endress, 1995), and a number of Poales, e.g., Centrolepidaceae (Sokoloff et al., 2009), Typhaceae (Müller-Doblies, 1970), and some Cyperaceae (Richards et al., 2006; Vrijdaghs et al., 2010); in basal eudicots in *Euptelea* and *Achlys* (Ranunculales) (Endress, 1969, 1986a, 1989b; Ren et al., 2007), in *Trochodendron* (Trochodendrales) (Endress, 1986a; Wu et al., 2007), in male *Styloceras* (von Balthazar and Endress, 2002a, b) and *Didymeles* (both Buxales) (von Balthazar et al., 2003); in core eudicots especially in the still poorly synorganized Saxifragales, such as Altingiaceae (Wisniewski and Bogle, 1982), Cercidiphyllaceae (Endress, 1986a; van Heel, 1987), and some Hamamelidaceae (Endress, 1978). In contrast, in higher core eudicots, it is much more rare and is known from some wind-pollinated Betulaceae (Abbe, 1974) and Myricaceae (Macdonald, 1977), the parasitic

Balanophora (female flowers) (Fagerlind, 1945), and the water plant *Callitriche* (Leins and Erbar, 1988).

Sepals that lose their protective function for floral buds may become much narrower and may greatly increase in number and take over a function in dispersal biology. This is well known from the pappus of Asteraceae (Semple, 2006) and the bristles in Cyperaceae (Schaffner, 1934), in which the protective function is exerted by bracts (in Asteraceae, in addition, by the valvate petals). Also in a number of Acanthaceae-Thunbergioidee (see above) the sepals that lost their protective function have decreased in size but increased in number (Schönenberger and Endress, 1998).

An interesting consequence of the loss of the perianth is that the position and number of stamens (and sometimes carpels) often becomes highly labile (Endress, 1990). There are many examples among the taxa mentioned earlier in this section, such as *Lindera*, *Litsea*, Pandanaceae, Typhaceae, *Euptelea*, *Achlys*, *Styloceras*, and *Trochodendron*.

ANDROECIUM

Stamen arrangement—As for the perianth organs, the most common stamen arrangement in monocots and core eudicots is in two whorls, the organs of the outer whorl in the sepal sectors and those of the inner whorl in the stamen sectors, thus with continuous alternation of the organs in the four whorls (diplostemonous flowers). If the alternation of the stamen whorls appears to be reversed, such flowers are called obdiplostemonous. However, detailed developmental studies show that obdiplostemony is not so easy to substantiate because of subtle changes during development (Leins, 1964b; Eckert, 1966; reviews in Ronse Decraene and Smets, 1995, and Endress, 2010b). In euasterids, there is only one whorl of stamens, alternating with the petals. In some basal angiosperms and basal eudicots, the stamens show a spiral phyllotaxis or are arranged in several whorls, sometimes in complex whorls by double and multiple positions (Endress and Doyle, 2007) (see Floral phyllotaxis). Arrangement patterns can be more complex or irregular, especially in flowers in which numerous stamens arise in groups on primary androecial primordia, a developmental pattern especially evolved in a number of larger clades in eudicots (see below).

Increase and decrease in stamen number—The number of stamens is increased and decreased in many clades, and it is especially labile and diverse in basal angiosperms. In the ANITA grade, stamen number is medium in Amborellaceae (12–21; Endress and Igersheim, 2000b), medium to small in basal Nymphaeales (1 in Hydatellaceae, 4–18 in Cabombaceae; Williamson and Schneider, 1993; Rudall et al., 2007), but highly increased in Nymphaeaceae (up to 200; Schneider and Williamson, 1993), medium to highly increased in Austrobaileyales (up to 300 in Schisandraceae; Saunders, 1998), and small (1) in Chloranthaceae and Ceratophyllaceae (Endress, 1987b, 2004). Also in magnoliids, there is a large range of stamen numbers with a number of inceases to numerous stamens (e.g., 1800 in Monimiaceae [Lorence, 1985] or several hundred in Annonaceae [Couvreur, 2009]) and decreases to two or three stamens in Piperaceae. Among monocots, increased numbers are present in Alismatales (up to over 30 in Alismataceae, Salisbury, 1926), in Pandanales (up to more than 50 in Velloziaceae [Sajo et al., 2010], up to 150 in Cyclanthaceae [Dahlgren et al., 1985], or up to many hundred in Pandanaceae [Huynh, 1991]), in Arecales (up to more than 900 in *Phytelephas*, Dransfield et al., 2008), and in Poales (up to 120 in *Ochlandra*, Soderstrom and Londoño, 1988). Among basal eudicots, the highest stamen numbers are in Ranunculaceae (*Laccopetalum* with up to more than 2000, Tamura, 1995), Papaveraceae (*Romneya* with up to 700, Karrer, 1991), and Nelumbonaceae (up to 400, Hayes et al., 2000). In rosids, peaks are, e.g., in Malpighiales (*Caryocar* with up to 750 [Prance, 1976] and *Hypericum* with up to 650 [Robson, 1996]) and Malvales (*Adansonia* with up to over 1000, Janka et al., 2008), and in the asterid lineage in Caryophyllales (Aizoaceae, *Cylindrophyllum* with ca. 2000 [Hartmann, 1993]; Cactaceae with ca. 4000 [Barthlott and Hunt, 1993]) and Ericales (Lecythidaceae, *Gustavia* with up to 1200 stamens and *Lecythis* with up to 1000 [Prance and Mori, 2004]). In lamiids and asterids, polystemony is almost absent, but is pronounced in Araliaceae (Endress, 2002; Jabbour et al., 2008; Nuraliev et al., 2010). Excessively high stamen numbers occur predominantly in brush flowers, which are pollinated by large animals (sphingids, birds, bats) or in beetle-pollinated flowers. Large numbers of stamens can easily be accommodated on a relatively small floral base because the filaments are thin in advanced groups. In basal angiosperms, however, the floral base needs to be greatly expanded because the stamens are more bulky. For instance, in *Tambourissa* (Monimiaceae), the floral diameter conspicuously changes with stamen number (Endress and Lorence, 1983; Lorence, 1985; Endress, 1987c). In several basal angiosperms, the innermost stamens are sterile (inner staminodes) and have attained special functions in pollination biology (Endress, 1984; Saunders, 2010), whereas inner staminodes are more rare in derived groups (Ronse Decraene and Smets, 2001).

Androecia with primary ring primordium or sectorial primordia together with increase in stamen number—In flowers with an increased stamen number among monocots and eudicots, the stamens are often not in a spiral or in simple or complex whorls but appear more irregularly positioned. During the development of such flowers, often at first a primary androecial ring primordium is formed. On this primary primordium, secondary primordia give rise to stamens. The stamen primordia appear in centripetal, centrifugal, or bidirectional sequence (Fig. 3C) (Ronse Decraene and Smets, 1992; Endress, 2006). Interestingly, a differentiation in primary and secondary primordia appears to be lacking in basal angiosperms. In basal eudicots, only cases with a centripetal initiation of secondary primordia are evident (perhaps with the exception of *Podophyllum* in Berberidaceae, deMaggio and Wilson, 1986); reported cases are in polystemonous Papaveraceae (*Romneya*, *Papaver*, Merxmüller and Leins, 1967; Karrer, 1991) and in Nelumbonaceae (Hayes et al., 2000). Among the two largest families resulting from the split of the former Flacourtiaceae, initiation is bidirectional in Achariaceae, but centrifugal in Salicaceae (Bernhard and Endress, 1999). Among Hamamelidaceae, it is centripetal in *Matudaea*, but centrifugal in *Fothergilla* (Endress, 1976), the two genera being in different subclades (Magallón, 2007). Among rosids and asterids, initiation is commonly centrifugal. Examples are in Fabaceae (Tucker, 2003b), Capparaceae (Leins and Metzenauer, 1979), Malvaceae-Bombacoideae (van Heel, 1966; Janka et al., 2008), and Bixaceae (Corner, 1946; Ronse Decraene, 1989), among Dilleniaceae in *Dillenia* (Corner, 1946; Endress, 1997; Tucker and Bernhardt, 2000), and among asterids in Lecythidaceae (Endress, 1994a; Tsou and Mori, 2007) and Theaceae (Tsou, 1998).

Instead of forming a continuous ring, the primary primordium can also appear subdivided into several (often five) sectors around the flower. Stamen initiation is also mostly centrifugal in these cases. It has been reported from Paeoniaceae (Hiepko, 1965a), Hypericaceae (Leins, 1964a), and various Malvales such as Malvaceae (van Heel, 1966; von Balthazar et al., 2004; 2006) and Cistaceae (Nandi, 1998). Both patterns, ring and subdivision in sectors, may occur in the same family (e.g., Dilleniaceae [Endress, 1997; Tucker and Bernhardt, 2000; Horn, 2009]; Clusiaceae [Ronse De Craene and Smets, 1991; Hochwallner and Weber, 2006; Sweeney, 2008]; Malvaceae [Janka et al., 2008]). In Myrtaceae, stamen initiation is centripetal, not centrifugal (e.g., Orlovich et al., 1999; Bohte and Drinnan, 2005). Loasaceae and Hydrangeaceae, both in Cornales, share diverse directions of stamen initiation (Hufford, 1990, 1997b, 1998). In many instances in flowers with sectorial primary primordia, the mature stamens form fascicles; this is especially conspicuous in some Malpighiales and malvids (Endress, 2010a), such as Clusiaceae (Sweeney, 2008), Euphorbiaceae (Prenner et al., 2008), Myrtaceae (Orlovich et al., 1999; Bohte and Drinnan, 2005), and Malvaceae (Janka et al., 2008).

Anther structure—Anther structure is conservative in angiosperms. The vast majority of anthers are differentiated into two lateral thecae, each with two pollen sacs, each theca opening by a longitudinal slit (stomium) between the two pollen sacs, and this through all major clades (Fig. 4A–D). However, there are some deviations from this ground pattern, which are often connected with special methods of pollen dispersal, such as cleistogamy or buzz pollination (survey of these deviations in Endress and Stumpf, 1990). It is puzzling that a number of apparently unrelated families of parasitic plants have such deviations in anther structure, such as Rafflesiaceae in Malpighiales, Apodanthaceae in Malvales or Cucurbitales, Santalaceae in Santalales, and Mitrastemonaceae in Ericales.

In the ANITA grade, in magnoliids and some basal eudicots, the connective is often thick and broad, the stamens (anthers) being cuneate and with a square or rectangular shape in transverse section (Fig. 4A, B). However, in core eudicots and monocots, there is a strong tendency for the connective to become thinner, and the pollen sacs concomitantly become bulging (Fig. 4C, D). The pattern of anther dehiscence is correlated with this change. Whereas anthers with a thin connective easily open by simple longitudinal slits, anthers with a thick connective sometimes need additional dehiscence lines and open with H-shaped or simple valves (Endress and Hufford, 1989; Hufford and Endress, 1989; Endress, 2008b). In a few clades of the ANITA grade, in many magnoliids, and in some basal eudicots, valves are present (Endress, 1994b), whereas they are lacking in monocots and core eudicots (except Hamamelidaceae) (Endress, 1989a). Thus, anthers with valvate opening occur almost exclusively in basal angiosperms and basal eudicots (plus Hamamelidaceae). Also, a comparatively large number of fossil stamens from the Early and Late Cretaceous have thick connectives and valvate dehiscence and are cuneate or wedge-shaped (Friis et al., 1988, 1991, 2006, 2010a, b; Friis and Endress, 1990; Endress and Friis, 1991; Magallón-Puebla et al., 1996, 1997; Magallón et al., 2001; Crepet et al., 2005; von Balthazar et al., 2007). Because this conspicuous anther form appears to be absent in the earliest angiosperm fossil record but becomes abundant

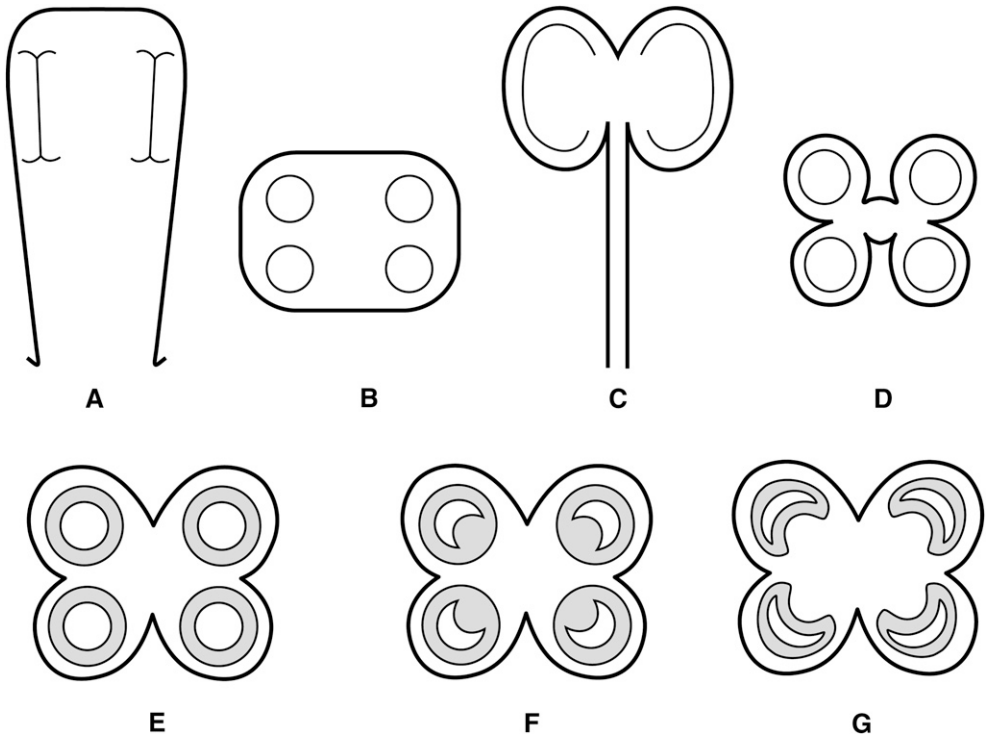

Fig. 4. (A–D) Different stamen shapes. (A, C) Ventral view. (B, D) Transverse sections. (A, B) Stamen cuneate, thecae opening with H-shaped valves (thin lines in A). (C, D) Stamen with bulging pollen sacs, thecae opening with longitudinal slits (thin lines in C). (E–G) Shape of sporogenous tissue in transverse sections of anthers. Tapetum shaded gray. (E) Pollen sacs without placentoid. (F) Pollen sacs with tapetal placentoid. (G) Pollen sacs with parenchymatic placentoid.

slightly later (Friis et al., 2010b), it may be not ancestral but represent an early evolutionary specialization, perhaps triggered by destructive insect pollinators (Endress 2008b).

The sporogenous tissue in each pollen sac is usually ovoid or elongate and thus round in transverse section (Fig. 4E). This simple shape may be deformed by a pollen sac placentoid (Hartl, 1963), which is a parenchymatic or tapetal protrusion into the sporogenous tissue from the center of the anther or theca by which the sporogenous tissue attains a crescent shape in transverse section (Fig. 4F, G). A pollen sac placentoid is mostly associated with the presence of numerous ovules and probably numerous pollen grains. An explanation for this association may be that the presence of a placentoid increases the surface area between tapetum and sporogenous tissue and that a sufficiently large surface area may be crucial for the maintenance of the synchrony of the meiotic process in each pollen sac (Heslop-Harrison, 1972). In addition, presence of numerous ovules requires production of numerous pollen grains and thus a large sporogenous tissue. However, the pollen sac placentoid also has an interesting systematic distribution. In the core eudicots, it mainly characterizes Lamiales and is very rare in other groups (Hartl, 1963; Endress, 2010a). But it also occurs in several families of monocots from different orders, such as Dioscoreales (Burmanniaceae, Rübsamen, 1986), Asparagales (Orchidaceae, Hartl, 1963; Rübsamen, 1986; Sood and Mohana Rao, 1988), Commelinales (Philydraceae, Hamann, 1966), and Zingiberales (Costaceae, Leinfellner, 1956).

SYNORGANIZATION BETWEEN PERIANTH AND ANDROECIUM

The simplest synorganization between perianth and androecium tends to occur in trimerous flowers with two perianth organ whorls and two stamen whorls. Because these whorls alternate with each other, the flower has sectors, each with a stamen and a closely associated perianth organ. These tend to form six complex units by basal fusion. This sectorial differentiation is well known in monocots (Endress, 1995), but it occurs likewise in a number of basal eudicots, especially core Ranunculales with trimerous flowers (Endress, 2010a) (Fig. 2C). Interestingly, these complex units remain together when the flower switches from trimery to pentamery (Fig. 2D), and the original alternation of organs from whorl to whorl is no longer present. This is illustrated by the rare pentamerous flowers in both groups. Among monocots, it is the case in *Pentastemona* (van Heel, 1992; Endress, 1995; Rudall et al., 2005) and among basal eudicots in pentamerous terminal flowers in the botryoids of *Berberis* (Endress, 1987a) and in the pentamerous flowers of Sabiaceae, in which the superposition of stamens and perianth parts has been difficult to understand (Endress, 2010a) if they were not seen in this context. The close association of each stamen with a perianth organ appears to provide an economical condition for bud protection, especially in flowers with valvate petals (e.g., Vitales, Santalales). In monocots, it has also become variously involved in pollination biology, e.g., in providing several accesses to the nectar (revolver flowers), in Sabiaceae potentially for the explosive mechanism (Ronse De Craene and Wanntorp, 2008). Fusion of the stamens with the petal tube in sympetalous flowers (stapet) is prominent in asterids, especially in some Ericales, in Gentianales, Lamiales, Solanales, Boraginaceae, and Asterales (Endress, 2010a) and often also takes part in revolver-flower architectures (Endress, 1994a).

A corona, an additional organ complex between the perianth and androecium, evolved in several monocots and core eudicots. Its formation begins somewhere in the androecium or the corolla in evolutionary terms and may lead to a relatively independent organ complex. It is variously involved in pollination biology. In monocots, it is especially well known in the Amaryllidaceae (Schaeppi, 1939) and Velloziaceae (Sajo et al., 2010) and in core eudicots in Apocynaceae (Endress and Bruyns, 2000; Kunze, 2005). Synorganization between petals and stamens may also be present by smaller petal appendages or other elaborations that are involved in nectar protection and canalization (Brown and Terry, 1992; Endress and Matthews, 2006b; Endress, 2010a).

GYNOECIUM

The gynoecium is the central and most complex part of flowers. It originates from the remaining floral apex, which is transformed into a gynoecium primordium in its entirety. There are numerous evolutionary trajectories in gynoecium structure. The structural units are the carpels containing the ovules. The carpels are cup-shaped (ascidiate) or plicate organs, or often mixed, proximally ascidiate and distally plicate, and with the ovules originating close to their margins. During development, the carpels become closed and sealed with the ovules inside (angiospermy). This sealing originates either by a secretion or by postgenital fusion of the flanks (Endress and Igersheim, 2000a). The distribution of different carpel forms and different patterns of angiospermy in basal angiosperms shows that most likely ascidiate carpels and angiospermy by secretion were ancestral in the angiosperms, as they are predominant in the ANITA grade (Doyle and Endress, 2000; Endress and Igersheim, 2000a; Endress, 2001b, 2005a; Endress and Doyle, 2009). At anthesis, pollen grains germinate at the receptive surface (the stigma), and pollen tubes grow down into the ovary to reach the ovules for fertilization. There is mostly a distinct pollen-tube transmitting tract from the stigma to the ovules, in which the pollen tubes grow and in which pollen tube competition takes place (Mulcahy, 1979; Erbar, 2003). This tract is commonly close to the inner morphological surface of the carpel (Endress and Igersheim, 2000a).

Intercarpellary fusion (syncarpy) and the advent of a compitum—In the majority of angiosperms, the carpels of a flower are congenitally united (syncarpous), and the separate pollen-tube transmitting tracts of all carpels are united into one (a compitum) at least for part of their course (Fig. 5C). This enables regular distribution of pollen tubes among the carpels if separate stigmas were unequally provided with pollen, and more importantly, it enables centralized pollen tube selection, which is superior to separate selection in each carpel (Endress, 1982; Armbruster et al., 2002). The advent of syncarpy and an intragynoecial compitum was a key innovation in angiosperm evolution. This key innovation evolved at least twice, in monocots (Buzgo and Endress, 2000; Igersheim et al., 2001) and in eudicots. Whereas the majority of clades in the ANITA grade and in the magnoliids and many basal eudicots are apocarpous (Fig. 5A, B, D) or unicarpellate, monocots and core eudicots are largely syncarpous (probably more than 80% of the angiosperm species; Endress, 1982). There are only a few magnoliids with syncarpy and an intragynoecial compitum, more in the Canellales-Piperales clade than in the Magnoliales-Laurales clade (Canellaceae,

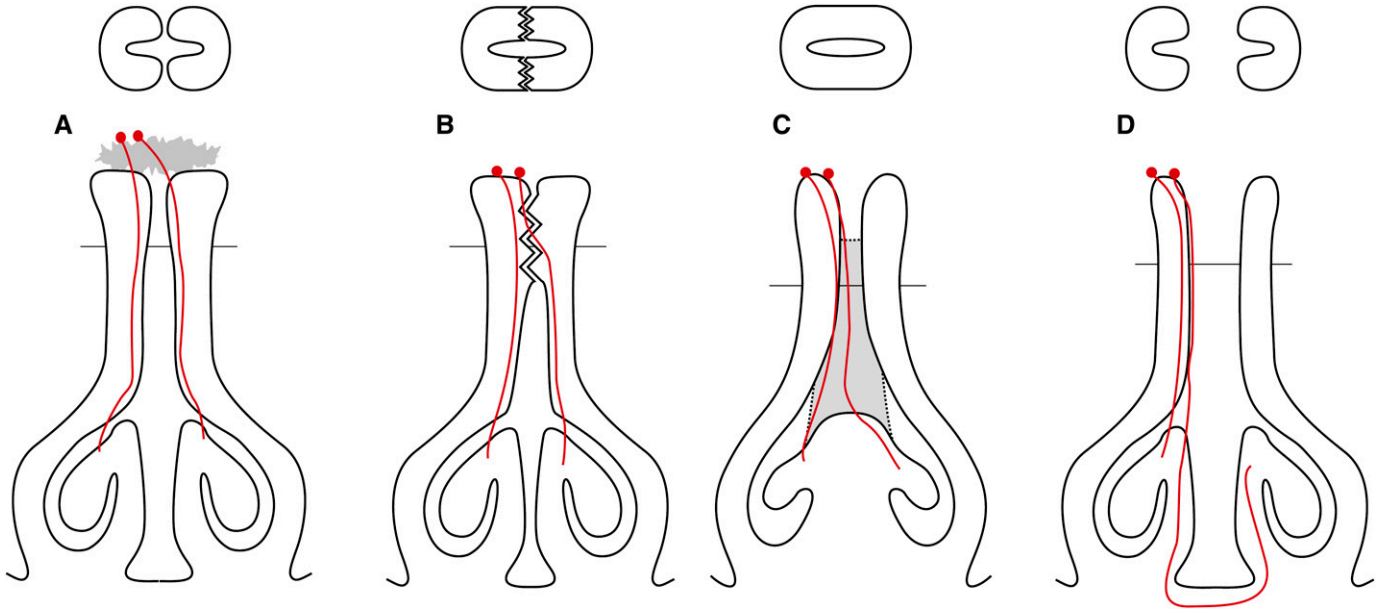

Fig. 5. Different forms of compitum in apocarpous and syncarpous gynoecia. Lower figures: median longitudinal sections. Upper figures: Transverse sections at level indicated in lower figures. Pathway of pollen tubes red, showing potential to cross from one carpel to the other. (A) Apocarpous gynoecium with extragynoecial compitum (in stigmatic secretion, gray). (B) Apocarpous gynoecium with compitum by postgenital fusion of carpel tips. (C) Syncarpous gynoecium with intracarpellary compitum (gray). (D) Apocarpous gynoecium with pollen tube crossing to another carpel via the floral base.

Takhtajania of Winteraceae, Aristolochiaceae and Piperaceae, the latter with uniovulate gynoecia; Endress and Igersheim, 1997, 2000a; Igersheim and Endress, 1997, 1998; Endress et al., 2000). As in apocarpous gynoecia, also in syncarpous gynoecia, the carpels are often ascidiate (synascidiate) proximally and plicate (symplicate) distally (Leinfellner, 1950). Because the pollen-tube transmitting tract usually differentiates close to the inner morphological surface of the carpel, it is restricted to the symplicate zone and the plicate zone (if the tips of the carpels are free), and the compitum to the symplicate zone. At a closer look, the advent of syncarpy somewhat preceded that of an intragynoecial compitum (Fig. 1). Syncarpy was a precondition for an intragynoecial compitum, but it also has other advantages over apocarpy, as discussed in Endress (1982). Another evolutionarily important aspect of pollen tube growth is its higher speed in derived groups compared with basal angiosperms (Williams, 2009; Williams et al., 2010).

Here and there, secondary apocarpy evolved in monocots (Alismatales, Endress and Doyle, 2009; Triuridaceae, Rudall and Bateman, 2006) and in core eudicots (e.g., among rosids in Rosaceae, Sapindales, and Malvaceae, and among asterids in Apocynaceae; Endress et al., 1983), which seems counterintuitive in view of the concomitant loss of the intragynoecial compitum. Interestingly, in most of these cases, a compitum has secondarily formed in another way. In apocarpous Sapindales, Malvaceae and Apocynaceae, the carpel tips become postgenitally united, and provide a compitum (Endress et al., 1983); in Tofieldiaceae (Alismatales), larger parts of the carpels are involved (Igersheim et al., 2001, Remizowa et al., 2006) (Fig. 5B). Postgenital fusion of partially free carpels also occurs in some Crossosomatales (Matthews and Endress, 2005b). Another possibility of a kind of a compitum is connection of stigmas by secretion or mere contiguity by which pollen tubes may pass from one carpel to another (extragynoecial compitum) (Fig. 5A). This has been reported in a number of basal angisperms, e.g., in the ANITA grade, in *Amborella* (Endress and Igersheim, 2000a; Williams, 2009), *Nymphaea* (Schmucker, 1932; Endress, 1982), Austrobaileyaceae (Endress, 1980b), Illiciaceae (Williams et al., 1993), Schisandraceae (Igersheim and Endress, 1997; Lyew et al., 2007), and in magnoliids in Annonaceae (Endress, 1982; Deroin, 1991), Himantandraceae (Igersheim and Endress, 1997), Calycanthaceae (Staedler et al., 2009), Atherospermataceae, Monimiaceae (Endress, 1980a), and Siparunaceae (Endress, 1980a; Renner et al., 1997). Curious, unusual cases of pollen tube pathways in which equal distribution of pollen tubes may be achieved were found in Alismataceae and Triuridaceae, both with numerous free and uniovulate carpels. In *Ranalisma* and *Sagittaria* (Alismataceae), surplus pollen tubes in a carpel leave the carpel via the floral base and grow from there into another carpel, which may not yet be provided with a pollen tube (Wang et al., 2002, 2006) (Fig. 5D). In cleistogamous flowers of *Lacandonia* (Triuridaceae), pollen germinates in the anther, and pollen tubes grow through the stamen filament into the floral base and reach the carpels from there (Márquez-Guzmán et al., 1993). It may be expected that there are also chasmogamous flowers in *Lacandonia* in which the mechanism is similar as in the mentioned Alismataceae.

Increase and decrease of carpel number—In monocots, the number of carpels is most often three and in core eudicots between two and five; thus, it is stabilized within a relatively narrow range of low numbers in these two most diverse angiosperm clades. In contrast, the range is much broader in the ANITA grade, in magnoliids and in basal eudicots (Endress, 1990). Stabilization to a low carpel number is highly correlated with a syncarpous gynoecium (and presence of a compitum), probably because a number higher than about five is more difficult architecturally to be accommodated in a whorl to still allow an efficient compitum (Endress, 2006). Vice versa, higher carpel numbers are often correlated with apocarpy, because due

to the lack of a precise compitum, there is much less constraint for carpel position. The carpels are then often arranged in several whorls or in a spiral. Especially high numbers have been recorded from Monimiaceae (2000 carpels in flowers of *Tambourissa ficus*, Lorence, 1985) and Ranunculaceae (10 000 carpels in *Laccopetalum giganteum*, Tamura, 1995). Among flowers with syncarpous gynoecia, the highest number of carpels ("only" up to 200) occurs in *Tupidanthus calyptratus* (Araliaceae) (Endress, 2002; Sokoloff et al., 2007).

Reduction in carpel number may lead to unicarpellate gynoecia. This extreme form is also relatively common in basal angiosperms with an apocarpous basic disposition and occurs there sporadically in most major groups (Hydatellaceae, Chloranthaceae, Ceratophyllaceae, Myristicaceae, Degeneriaceae) and characterizes an especially species-rich family, the Lauraceae (Endress, 1972) and its probable sister, Hernandiaceae (Endress and Lorence, 2004). In basal eudicots, unicarpelly characterizes Berberidaceae, Proteaceae, and Didymelaceae, and in core eudicots especially the species-rich family Fabaceae (Tucker, 2003a) but is otherwise not common. In contrast, gynoecium reduction in core eudicots and monocots leads more often to pseudomonomerous gynoecia, which have a single functional carpel together with sterile remnants of additional carpels. There may be developmental constraints for a pluricarpellate syncarpous gynoecium to evolve into a completely unicarpellate structure (e.g., Müller-Doblies, 1970). The diversity and distribution of pseudomonomerous gynoecia in angiosperms are shown in a comparative account by Eckardt (1937), with a special focus on the former Urticales (now in Rosales). Pseudomonomery was studied and discussed in additional clades in the meantime, e.g., among monocots in Typhaceae (Müller-Doblies, 1970), Poaceae (Philipson, 1985), and Restionaceae (Ronse Decraene et al., 2002), all three in Poales, among rosids in Anacardiaceae (Bachelier and Endress, 2007, 2009), Chrysobalanaceae (Matthews and Endress, 2008), and Corynocarpaceae (Matthews and Endress, 2004), and among asterids in Acanthaceae (Schönenberger and Endress, 1998) and Metteniusaceae (González and Rudall, 2010). A new comparative treatment of pseudomonomery would be timely.

Ovary position—One of the frequently mentioned kinds of diversity in angiosperm flowers is the shifting position of the ovary: superior and inferior (Fig. 6A, B). Inferior ovaries develop when the floral apex is not convex or flat but becomes concave during or after perianth formation, with the result that the lower part of the gynoecium appears sunken into the floral base in the anthetic flower (Soltis and Hufford, 2002). It has been argued that an inferior ovary position is favored in flowers pollinated by animals with potentially destructive mouth parts, such as beetles or birds (Grant, 1950). It can also be seen as a more economical architecture than a superior ovary with a floral cup because the two protective structures, ovary wall and floral cup, are combined into one.

Inferior ovaries, earlier believed to be a derived feature, and especially common in evolutionarily advanced angiosperms, are today seen as evolutionarily quite flexible, as many reversals from inferior to superior have been found (review in Endress, in press), and because inferior ovaries are also present in a number of basal angiosperms. Among the ANITA grade they occur in some Nymphaeaceae (Schneider and Williamson, 1993, Borsch et al., 2008) and *Hedyosmum* (Chloranthaceae) (Endress, 1987b); among magnoliids in Eupomatiaceae (Endress, 1977; Igersheim and Endress, 1997), Gomortegaceae, Hernandiaceae, Lauraceae p.p., *Tambourissa* of Monimiaceae (Endress, 1980a; Endress and Lorence, 1983; Endress and Igersheim, 1997), and Aristolochiaceae (Igersheim and Endress, 1998); among basal monocots in some Alismatales (Hydrocharitaceae) (Igersheim et al., 2001); and among basal eudicots (only partly inferior) in Papaveraceae (*Platystemon*) and Trochodendraceae (*Trochodendron*) (Endress, 1986a; Endress and Igersheim, 1999). In more advanced groups, among monocots, it characterizes many Dioscoreales and all Zingiberales, in Asparagales, e.g., Amaryllidaceae, Doryanthaceae, Hypoxidaceae, Iridaceae, and Orchidaceae (e.g., Kocyan and Endress, 2001a, b; Rudall, 2002b), and among core eudicots, e.g., the Cucurbitales-Fagales clade, Santalales, Rubiaceae, Dipsacales, and most Asterales (Endress, 2010a).

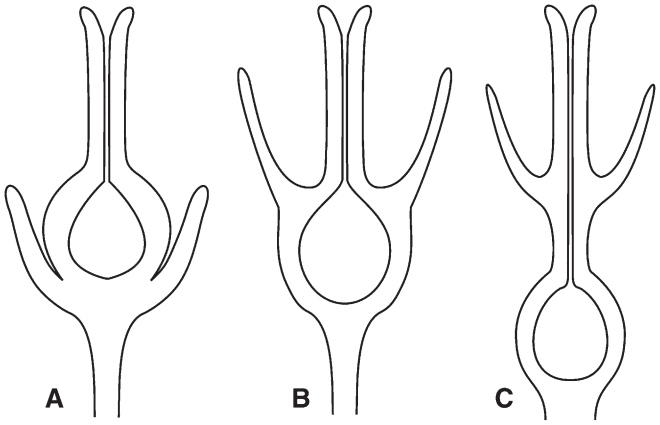

Fig. 6. Different ovary positions. Longitudinal sections. (A) Superior. (B) Inferior. (C) Inferior with neck.

A further accentuation of the inferior ovary position is the formation of a neck, i.e., the elongation of the inferior zone above the ovary locules (Fig. 6C). A neck evolved repeatedly in monocots and eudicots (Endress, 1995, 2010a): among monocots in at least three orders, in Alismatales (several Hydrocharitaceae, Troll, 1931; Tomlinson, 1969; Endress, 1995), Asparagales (some Amaryllidaceae, Hypoxidaceae, Orchidaceae, and Iridaceae, Wunderlich, 1950; Traub, 1975; Goldblatt, 1986; Burtt, 2000; Kocyan and Endress, 2001a, b), Zingiberales (Lowiaceae, Strelitziaceae, Kirchoff and Kunze, 1995; Kronestedt and Walles, 1986; Kirchoff, 1998), and among eudicots especially in the Cucurbitales-Fagales clade (Matthews and Endress, 2004; Endress, 2010a), but also in Myrtales (some Onagraceae, Eyde and Morgan, 1973; and Combretaceae, Correll and Correll, 1982), some Dipsacales (Wilkinson, 1948; Fukuoka, 1972), and a few Asteraceae-Lactuceae (Wagenitz, 1979).

Bulging of ovaries and apical septum—Another kind of specialization in ovary structure is bulging of the ovary wall around the ovule(s). Bulging has evolved in numerous groups of angiosperms with mainly uniovulate carpels, especially in monocots and core eudicots. Either the entire ovary wall bulges or only the locule. In the first case, the bulge is visible from the surface of the gynoecium; in the second case, it is only visible from the inside of the ovary. Bulging occurs in apocarpous and syncarpous gynoecia.

Apocarpous gynoecia with bulged ovaries (Fig. 7A, B) are present among basal angiosperms in Schisandraceae and Winteraceae (*Drimys*) (Leinfellner, 1966; Igersheim and Endress, 1997). The cases in monocots, Alismataceae (Eckardt, 1957;

Igersheim et al., 2001) and Triuridaceae (Rübsamen-Weustenfeld, 1991; Igersheim et al., 2001), and some eudicots, such as Ranunculaceae (Eckardt, 1957; Rohweder, 1967) and Rosaceae (*Potentilla*, *Alchemilla*, *Prinsepia*, *Potaninia*; Juel, 1918, 1927; Schaeppi and Steindl, 1950) are all similar because they are associated with increase in carpel number and decrease in carpel size. An apocarpous bulged rosid family with only five or a single carpel are Surianaceae (*Suriana*, Bello et al., 2007; *Stylobasium*, Carlquist, 1978).

Syncarpous gynoecia with bulged ovaries (Fig. 7C, D) are present among monocots in Arecaceae (Geonomeae, only weakly syncarpous) (Stauffer et al., 2002; Stauffer and Endress, 2003); in rosids among, e.g., Coriariaceae (Matthews and Endress, 2004), Ochnaceae (Baum, 1951; Guédès and Sastre, 1981), Chrysobalanaceae (Matthews and Endress, 2008), Limnanthaceae (Hofmann and Ludewig, 1985), Sphaerosepalaceae (Horn, 2004), and Rutaceae (only very slightly syncarpous) (Hartl, 1962); and in the asterid alliance in Rhabdodendraceae (Puff and Weber, 1976), Phytolaccaceae (Eckardt, 1954; Rohweder, 1965), Boraginaceae (Hilger, 1981, 1984, 1985), and Lamiaceae (Junell, 1934). Such syncarpous gynoecia with bulged ovaries have often been misinterpreted as apocarpous (e.g., Coriariaceae, discussion in Matthews and Endress, 2004; Ochnaceae, discussion in Baum, 1951; Phytolaccaceae, discussion in Rohweder, 1965).

A morphological consequence of carpel bulging is that the length of the ovary (locules) is greatly reduced on the ventral side. In the extreme case, the ovary roof touches the ovary base (Fig. 7D) (Boraginaceae, see e.g., fig. 69, in Svensson, 1925; Verbenaceae, see e.g., fig. 8, in Junell, 1934). The potential significance of this strict canalization of the compitum to the ovary base by the immersed stylar canal is unknown.

In syncarpous gynoecia, bulging of the locule but not of the entire ovary wall is associated with an apical septum, a septum from the ovary roof that appears to be "perforated" by the continuation of the stylar canal in the center (Hartl, 1962) (Fig. 7D). An apical septum has also evolved many times in angiosperms, in monocots, e.g., in Hypoxidaceae (Kocyan and Endress, 2001a), in rosids, e.g., in Myrtaceae (Hartl, 1962) and Podostemaceae (Jäger-Zürn, 2003), and it is prominent in asterids, such as in Ericales, Boraginaceae, Lamiales, and Solanales (Hartl, 1962). In Boraginaceae and Lamiaceae, in addition to the apical septum, there are also "false septa" that partition each carpel into two parts, and each part bulges separately (see Gottschling, 2004); this is especially conspicuous because each of the four parts differentiates as a dispersal unit.

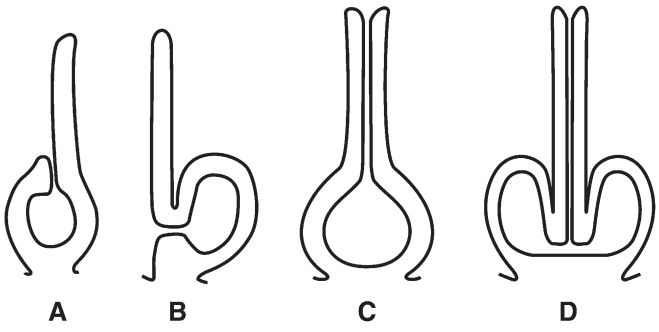

Fig. 7. Different ovary shapes. Longitudinal sections. (A, B) Free carpels. (A) Not bulging. (B) Bulging. (C, D) Syncarpous gynoecia. (C) Not bulging. (D) Bulging, forming an apical septum.

It may also occur in some other families without separate diaspore development, e.g., some Ericaceae (Palser, 1961), but this needs more study.

Architecture of pluriovulate ovary locules—Syncarpous ovaries with several or numerous ovules may be plurilocular or unilocular. Both architectures have functional advantags and disadvantages. Plurilocular ovaries provide more potential for elaborate dispersal mechanisms in fruit, whereas unilocular ovaries allow a higher degree of increase in ovule number because ovules can be better accommodated in an uncompartmented space. If numerous ovules are present, they are either on protruding diffuse (axile or free central) or ramified (axile or parietal) placentae. Protruding diffuse axile placentae reach a peak in asterids, especially lamiids, with Gentianales, Lamiales, and Solanales (Endress, 2010a). Examples of ramified axile placentae are prominent in Velloziaceae (Sajo et al., 2010), Gesneriaceae (Weber, 1971), and Bignoniaceae (Leinfellner, 1973), examples of ramified parietal placentae in Orchidaceae (e.g., *Aa*, Cocucci, 1965) or Cytinaceae (*Cytinus*, Igersheim and Endress, 1998). The relationships between ovary architecture and ovule number need more comparative study.

Ovules—Ovules are conservative organs, being the oldest morphological reproductive units of angiosperms (of the sporophytic generation) that can be traced back to early seed plants. Specific structural variants are relatively constant in larger clades of angiosperms, even more so than was earlier recognized, and are thus of special interest in macrosystematics, as will be explained in this chapter. If not stated otherwise, descriptions always relate to ovules with mature embryo sacs. It has long been known that angiosperm ovules have ancestrally two integuments (bitegmic) and that the nucellus is thick, i.e., with at least one hypodermal cell layer above the meiocyte (crassinucellar). Bitegmic crassinucellar ovules are present in the ANITA grade, in magnoliids, in most monocots, in basal eudicots, and part of the core eudicots. There is a trend to form less bulky ovules by reduction of the integuments to one (unitegmic) and of the nucellus thickness to just the epidermis above the meiocyte (tenuinucellar) in the angiosperms as a whole. Such unitegmic tenuinucellar ovules are characteristic in one large clade of core eudicots, the asterids, and bitegmic tenuinucellar ovules occur in various monocots (Rudall, 1997), but also in several smaller parts of other core eudicots, especially in some parasitic or mycotrophic groups. With the evolution of smaller ovules, another structural economization of the flower, more ovules can be produced in an ovary. Thus, plants become more flexible in ovule number per flower.

High ovule number may be especially critical in some highly specialized ecological situations, such as parasitism (e.g., Rafflesiaceae, Hydnoraceae) or epiphytism (e.g., Orchidaceae, Gesneriaceae), in which many of the wind-dispersed diaspores may not reach an appropriate site for establishment. Among parasites, Santalales are an interesting exception from the formation of numerous ovules per flower. Nevertheless, many Santalales form ovules without integuments (Fagerlind, 1948; Brown et al., 2010). In some Santalales, reduction of ovules is so radical that they are not even formed, and thus seeds are also lacking (Loranthaceae, Balanophoraceae, Fagerlind, 1948). In Balanophoraceae, the most extreme case, also the inner morphological surface of the gynoecium has completely disappeared so that the embryo sacs and embryos are formed directly in the compact gynoecium (Fagerlind, 1948). Santalales exhibit

two major evolutionary tendencies with respect to diaspores. In epiphytic groups (Loranthaceae, some Santalaceae), the fruit wall is sticky, and there is highly efficient seed dispersal by birds. In contrast, in the terrestrial Balanophoraceae, the female flowers, which consist only of an extremely reduced gynoecium, are greatly increased in number, a convergent trend to the increase in number of the ovules per flower in other groups of parasites. The occurrence of radical ovule reduction in the parasitic Santalales without increase of embryo sac number per gynoecium leads to the question whether ovule reduction in parasitic plants may also have other reasons, such as lacking need for a protective seed coat if germination takes place directly on the host (in many Santalales surrounded by the sticky fruit wall) (see also Kuijt, 1969). In the giant flowers of *Rafflesia* (Davis et al., 2007, 2008; Davis, 2008), the ovules are morphologically reduced as in other parasites (Bouman and Meijer, 1994), but they are secondarily increased in size as the entire flowers (Igersheim and Endress, 1998).

Recent comparative studies in ovules based on new original studies and on a broad literature review revealed new systematically interesting features (Endress and Igersheim, 2000a; Endress, 2003b, 2005b, 2010a; Endress and Matthews, 2006b) and also formerly largely unnoticed distribution patterns of earlier recognized features.

Nucellus differentiation (thickness)—Different degrees of the crassinucellar and tenuinucellar condition (in a similar way as distinguished by Hamann, 1977, and especially Shamrov, 1998) (Fig. 8A–F) were found to be correlated with clades at suprafamilial level (Endress, 2010a). (1) The wide occurrence of crassinucellar ovules and their ancestral nature in angiosperms has already been mentioned. In the present, finer classification, crassinucellar ovules have more than one hypodermal cell layer above the meiocyte (Fig. 8A). (2) Weakly crassinucellar ovules have only a single hypodermal cell layer above the meiocyte (Fig. 8B). Within the ANITA grade, they are only known from Cabombaceae (Igersheim and Endress, 1998) and are unknown from magnoliids. In monocots, they occur in most orders to some extent, from Alismatales upward, with peaks in Commelinales and Zingiberales in rosids. Among eudicots, they are especially prevalent in some Saxifragales, the COM clade of rosids (Matthews and Endress, 2002, 2004a; Endress and Matthews, 2006b), and in asterids mainly in Cornales, Boraginales, Solanales, and Bruniales (Endress, 2010a). (3) In pseudocrassinucellar ovules, there is no hypodermal cell layer above the meiocyte, but by periclinal divisions in the epidermis, the meiocyte attains a deeper position (Fig. 8C). Among the ANITA grade, it is only known in Hydatellaceae (see Rudall et al., 2008). It was not reported in magnoliids. In monocots, it occurs especially in Acorales and a number of Alismatales, a few Asparagales, and some Poaceae (Rudall, 1997; Igersheim et al., 2001), and in basal eudicots in some Papaveraceae and most Ranunculaceae (Endress & Igersheim, 1999). In rosids and asterids, it appears to be insignificant. (4) In incompletely tenuinucellar ovules, the meiocyte is hypodermal at the nucellus apex, but the nucellus contains hypodermal cell layers at the flanks and and/or below the meiocyte (Fig. 8D). Such ovules are absent in the ANITA grade, and in magnoliids they occur only in Piperales, but there in three families (Hydnoraceae, Lactoridaceae, and *Houttuynia* of Saururaceae; Bouman, 1971; Tobe et al., 1993; Igersheim and Endress, 1998). They are widespread in monocots, especially in Dioscoreales, Pandanales, and Poales, but also in some Liliales, Asparagales, and Commelinales. In basal eudicots, they are only known from Circaeasteraceae (Endress and Igersheim, 1999). In rosids, they mainly characterize the COM-clade and Brassicales (Matthews and Endress, 2002, 2004a; Endress and Matthews, 2006b); in asterids, they are widespread but do not occur in Gentianales (En-

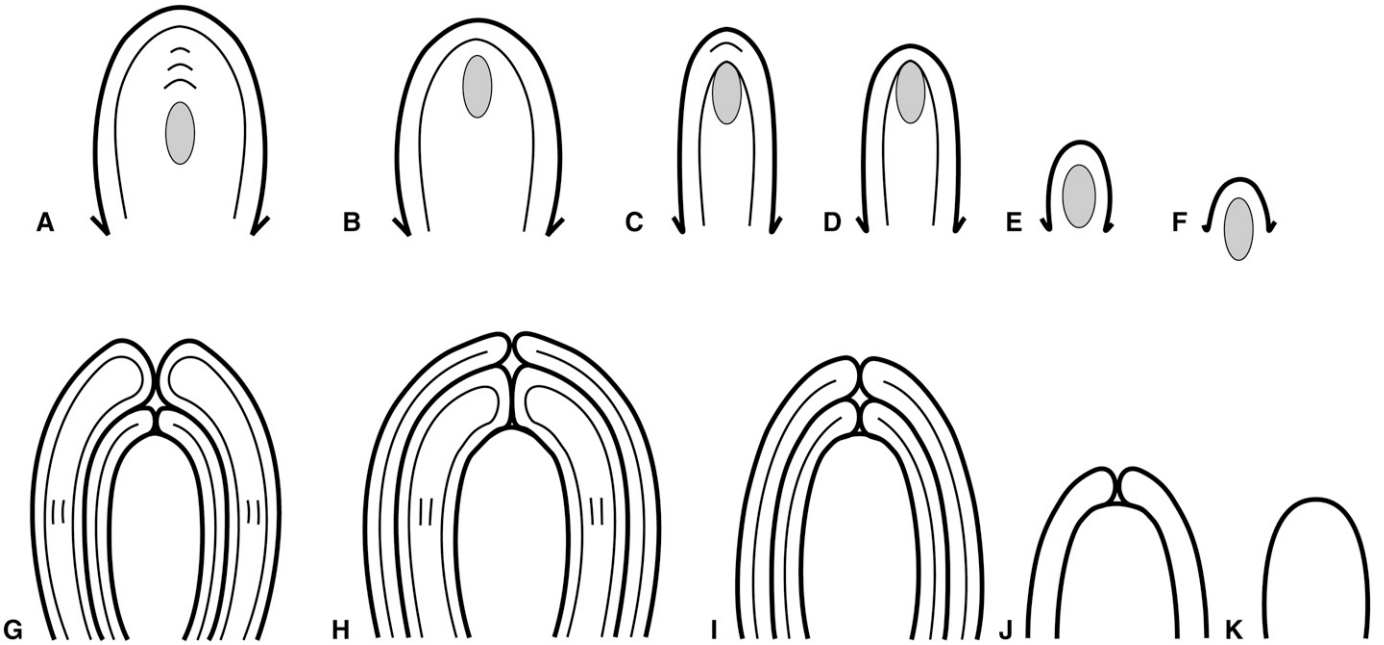

Fig. 8. Ovule diversity. Longitudinal sections. (A–F) Different nucellus shapes. Cell layers indicated by thin lines. Meiocyte shaded gray. (A) Crassinucellar. (B) Weakly crassinucellar. (C) Pseudocrassinucellar. (D) Incompletely tenuinucellar. (E) Tenuinucellar. (F) Reduced tenuinucellar. (G–K) Different integument differentiation. Cell layers indicated by thin lines. (G–I) Bitegmic. (G) Outer integument thicker than inner. (H) Inner integument thicker than outer. (I) Both integuments equally thick. (J) Unitegmic. (K) Ategmic.

dress, 2010a). (5) Tenuinucellar ovules (Fig. 8E), in which the meiocyte fills the entire nucellus below the epidermis occur especially in some species-rich clades of asterids (Gentianales, Lamiales, and Asteraceae) (Endress, 2010a), among monocots only in Orchidaceae (Asparagales) and Triuridaceae (Pandanales), both families mycotrophic. Tenuinucellar ovules consistently have only one integument (asterids) or two thin ones, two cell layers thick (monocots). (6) Reduced tenuinucellar ovules with the meiocyte halfway inferior (Fig. 8F) were found only in some Gentianales (Apocynaceae, Gentianaceae, and Rubiaceae), Lamiales (Gesneriaceae, Lentibulariaceae, and Plantaginaceae), and Solanales (Convolvulaceae) (Endress, 2010a). Thus, in this classification, the traditional crassinucellar encompasses (1) and (2), and the traditional tenuinucellar (3)–(6).

Another interesting trend of reduction in tenuinucellar ovules is that in some clades they do not contain a vascular bundle. This has been found in asterids especially in Gentianales and Lamiales and in monocots in Burmanniaceae (Dioscoreales), Triuridaceae (Pandanales), and Orchidaceae (Asparagales).

Integument number and differentiation (thickness)—Ovules have two integuments (bitegmic) (Fig. 8G–I) or one (unitegmic) (Fig. 8J); exceptionally, they do not have an integument (ategmic) (Fig. 8K). Bitegmic ovules are predominant in angiosperms. They characterize most basal clades, practically all monocots, and most rosids.

In bitegmic ovules, there are three possible dispositions: (1) The outer integument is thicker than the inner (Fig. 8G), (2) the inner integument is thicker than the outer (Fig. 8H), or (3) both integuments are equally thick (Fig. 8I). Angiosperm-wide, mostly the outer is thicker than the inner, or both are equally thick. The first is the case in most basal angiosperms (the inner integument is thicker only in Chloranthaceae without *Hedyosmum* and in all families of Piperales, and both are equally thick in *Barclaya* of Nymphaeaceae and Gomortegaceae; Endress and Igersheim, 1997; Igersheim and Endress, 1998). In monocots, diversity is especially narrow; the outer integument is thicker than the inner or—almost equally common—both integuments are equally thick; the inner integument is almost always only two cell layers thick. In my literature survey, I found only two monocot species with the inner integument thicker (at anthesis) than the outer, both in Asparagaceae-Brodiaeoideae (Berg, 1978, 1996). In Zingiberales, the outer integument is always thicker than the inner, and in Liliales and Asparagales predominantly so, whereas in Commelinales and Poales both integuments are more often equally thick. In basal eudicots, the outer integument is commonly thicker than the inner, but in Proteales (except *Nelumbo*) and Trochodendrales it is the other way around (Endress and Igersheim, 1999). In the rosid alliance, the outer integument is predominantly thicker than the inner in Saxifragales, Vitales, and the nitrogen-fixing clade, whereas it tends to be the other way around in malvids plus the COM clade (Endress and Matthews, 2006b), one of the arguments for the closer relationships of the two latter clades, as suggested by floral structure (Endress and Matthews, 2006b) and by mDNA studies (Zhu et al., 2007; Qiu et al., 2010). Equally thick integuments mainly characterize Geraniales (3 or 2–3 cell layers) and Myrtales (2 cell layers), but also occur at lower frequency in various other orders. Among the asterid alliance, in Caryophyllales, both integuments tend to be equally thick (Endress, 2010a); in those Ericales with two integuments, the inner tends to be thicker than the outer in the former Primulales, and the other way around in the other families (Endress, 2010a).

Unitegmic ovules (Fig. 8J) are rare in basal angiosperms. In addition to Ceratophyllaceae (e.g., Igersheim and Endress, 1998), they only occur in Siparunaceae (Endress, 1972; Endress and Igersheim, 1997; Kimoto and Tobe, 2003), *Peperomia* (Piperacae), and *Hydnora* (Hydnoraceae) (Igersheim and Endress, 1998). Among monocots, they occur in a few Alismatales, but records in other orders are very rare and mostly not well substantiated (Igersheim et al., 2001; Buzgo, 2001). In basal angiosperms, they are partially present in three families of core Ranunculales and in Sabiaceae (Endress and Igersheim, 1999). In core eudicots, they occur sporadically in a number of rosid orders, with a peak in the nitrogen-fixing clade, especially in Fagales (Endress and Matthews, 2006b). In the asterid alliance, unitegmic ovules are predominant by far. In the basal orders Santalales and Ericales, however, a number of subclades have retained the bitegmic state as well as the unplaced Icacinaceae and Vahliaceae, and possibly the derived Paracryphiales (Mauritzon, 1933; Endress, 2010a). In unitegmic ovules, the integument always has more than two cell layers (the water plant *Ceratophyllum* has only 2–3). Ategmic ovules (Fig. 8K) are extremely rare in angiosperms and were recorded in *Crinum* of Amaryllidaceae (Howell and Prakash, 1990) and in some Santalales and Gentianales (some saprophytic Gentianaceae and a Rubiaceae; Bouman et al., 2002; Endress, 2010a).

A broader comparative study on the correlation of integument differentiation at anthesis and seed coat differentiation at seed maturity in angiosperms is still lacking, although Corner (1976) provided extensive material for basal angiosperms and eudicots.

Ovule curvature and micropyle formation—Angiosperm ovules are mostly anatropous, more rarely campylotropous or orthotropous or hemitropous. Curved ovules are so predominant because ovule curvature allows positioning of the micropyle close to the placenta and thus easy access of the pollen tube to the micropyle in most kinds of ovary architecture. The pollen tube is guided to the tip of the nucellus by the micropyle, which is mostly formed by the inner integument or by both integuments in bitegmic ovules, or by the single integument in unitegmic ovules. A special kind of micropyles formed by both integuments are zig-zag micropyles, in which the outer integument overgrows the inner in a way that the two parts of the micropylar canal are not aligned but have a zig-zag shape. Zig-zag micropyles often go hand in hand with campylotropous ovules (Endress and Matthews, 2006b).

Anatropous ovules predominate by far in angiosperms. This is also true for basal angiosperms, although there are several groups with orthotropous ovules especially in the ANITA grade (Amborellaceae, *Barclaya* in Nymphaeaceae, and Chloranthaceae and Ceratophyllaceae; Endress and Igersheim, 1997; Igersheim and Endress, 1998), but fewer in the magnoliids (Gomortegaceae, and three families in Piperales: Hydnoraceae, Piperaceae, Saururaceae) (Endress and Igersheim, 1997; Igersheim and Endress, 1998). This relatively common occurrence of orthotropous ovules in the ANITA grade (and basal monocots, see below) can be explained by the more common internal secretion in carpels, and thus less canalized pathway of pollen tubes (Endress and Igersheim, 2000a). The strong secretion may be facilitated by their predominant occurrence in moist habitats (Endress and Igersheim, 2000a; Feild et al., 2009). Campylotropous ovules are restricted to Canellaceae among basal angiosperms (Igersheim and Endress, 1997). In monocots, most ovules are anatropous, but orthotropous in Acorales,

a number of Alismatales, some Asparagales, Commelinales, and Poales. Campylotropous ovules are rare (campylotropy is sometimes clearly expressed only after anthesis) and have a scattered distribution. Hemitropous ovules occur in some Commelinales and Poaceae. In basal eudicots, most ovules are also anatropous, a few are hemitropous. Orthotropous ovules are only known from Circaeasteraceae and many Proteales (not in Nelumbonaceae), campylotropous ovules mainly from Papaveraceae and Berberidaceae among Ranunculales (Endress and Igersheim, 1999). Among core eudicots, again, most ovules are anatropous. Orthotropous ovules are rare and occur especially in some wind-pollinated clades (e.g., Fagales, former Urticales, *Leitneria* in Simaroubaceae). Campylotropous ovules have peaks of occurrence in Fabales (Fabaceae, Surianaceae) and in the malvids (including the extended malvids of the Angiosperm Phylogeny Group, 2009). In the asterid alliance, campylotropous ovules are predominant in a number of major subclades, such as Caryophyllales, Santalales, Ericales, Garryales, Gentianales, Lamiales, Solanales, and Apiales. In several cases, they are anticampylotropous (curved in the reverse direction of the initial anatropous curvature), but this needs more comparative study (Endress, 2010a). Orthotropous ovules are very rare in the asterid alliance and occur mostly in highly reduced forms, especially in some Gentianales.

Micropyle types in bitegmic ovules are not randomly distributed but show some systematic patterns. A micropyle formed by the inner integument is especially common in the ANITA grade (Amborellaceae, Cabombaceae, part of Nymphaeaceae, most Austrobaileyales and part of Chloranthaceae) and in magnoliids (Endress and Igersheim, 1997; Igersheim and Endress, 1998), also in the majority of monocots (only in Poales more often by both integuments). This is also true for basal eudicots, although both integuments are involved in basal Ranunculales: Eupteleaceae and Papaveraceae and sporadically in some other orders (Endress and Igersheim, 1999). In contrast, in core eudicots micropyles formed by both integuments are predominant. Here especially, zig-zag micropyles have an interesting distribution being present mainly in Fabales on the one hand and in malvids plus the COM clade on the other (Endress and Matthews, 2006b). In contrast, in the asterid alliance in the clades with bitegmic ovules (Caryophyllales, Santalales, Ericales) the micropyle is mostly formed by the inner integument (Endress, 2010a).

SYNORGANIZATION BETWEEN ANDROECIUM AND GYNOECIUM

Secondary pollen presentation on the gynoecium—A conspicuous architecture based on the synorganization of androecium and gynoecium is pollen deposition on the style or the outside of the still closed and unreceptive stigmatic lobes and pollen collection by pollinators from there (Yeo, 1993). This specialization is mainly known from asterids, with peaks in some Ericales (epacrid Ericaceae), Gentianales (Loganiaceae, Rubiaceae), and Asterales (Asteraceae, Campanulaceae, Calyceraceae, Goodeniaceae) (Endress, 2010a). The most species-rich groups with secondary pollen presentation are Rubiaceae (over 10 000 species) and Asterales, especially Asteraceae (over 23 000 species). In Rubiaceae, pollen is deposited on a thickened apical or subapical part of the gynoecium, and in some cases, the stigma is below this part (as in Apocynaceae, see below) (Igersheim, 1993; Puff et al., 1996). In Asterales, there are no conspicuously thickened apical parts of the style, but the style is often coverd with hairs, in which pollen collects; the hairs are retractable in many Campanulaceae to get rid of pollen at the end of the male phase of anthesis. In Asteraceae and part of Campanulaceae (especially Lobelioideae), the anthers are postgenitally united and form a tube through which the style elongates and then presents the pollen it has carried up with it. In the different subclades, a diversity of structural variants and means of economical pollen presentation evolved (Erbar and Leins, 1995; Leins and Erbar, 2006, 2008).

Gynostemium or gynostegium and pollinarium formation—The most amazing result of the synorganization of androecium and gynoecium is the evolution of pollinaria, which took place at least twice in angiosperms, once in monocots in Orchidaceae (Asparagales) and once in eudicots in Apocynaceae (Gentianales). It is also a case of secondary pollen presentation, but is much more complex than in the groups mentioned above. Pollinaria consist of pollinia (the compact content of all pollen grains of a pollen sac) and a translator, a device that holds two or four pollinia together and attaches them to the body of a pollinator, either by a clip or by glue (Fig. 9C, F). A precondition for the evolution of pollinaria in both groups is the intimate synorganization between anthers and the uppermost part of the gynoecium. The pathway of synorganization is different in Orchidaceae and Apocynaceae. In Orchidaceae, it went via a gynostemium, i.e., by congenital fusion of gynoecium and androecium. A gynostemium is present in all Orchidaceae. However, a mere gynostemium was only a precondition, but not the trigger for the overwhelming diversification of orchids. Only the functional connection of the anthers and stigmatic lobes within the gynostemium resulting in the advent of pollinaria made this possible (Fig. 9D, E). This is evident in the fact that the "basal" clades Apostasioideae, Vanilloideae, and Cypripedioideae (Górniak et al., 2010) without pollinaria have not more than ca. 330 species in total, whereas the other major subclades of the family have pollinaria and have more than 20 000 species. The synorganization between anther and stigmatic lobes in these orchids has been shown in a number of studies (e.g., Vogel, 1959; Rasmussen, 1986; Kurzweil, 1987; Schick, 1988; Endress, 1994a; Rudall and Bateman, 2002). Monosymmetry and the ability of flowers to twist (resulting in resupination) were a first favorable evolutionary step (Rudall and Bateman, 2002) because this combination is also present in Apostasioideae, Vanilloideae, and Cypripedioideae (Kurzweil, 1993; Kocyan and Endress, 2001a). However, it also occurs in a number of other angiosperm families (Goebel, 1924). The potential of twisting is important in monosymmetric flowers in general to adjust the flower position in inflorescences to a perpendicular orientation. The propensity of orchid flowers to be deceptive (e.g., Cozzolino and Widmer, 2005; Schiestl, 2005), and thus, high pollinator-specificity, may have been caused by the advent of pollinaria because high pollinator-specificity is a precondition for the success of pollination with pollinaria. A gynostemium is not even a necessary precondition for pollinarium evolution, as shown by Apocynaceae, in which synorganization of gynoecium and androecium took another pathway. Here a "gynostegium", a postgenital fusion product between androecium and gynoecium, specifically between anthers and stigmas (Fig. 9A, B), led to the same evolutionary result, the advent of pollinaria (Kunze, 1993; Endress, 1994a; M. E. Endress, 2001; Fishbein, 2001) and may also have triggered rapid radiations (Meve and Liede, 2002; Rapini et al., 2007). In Apocynaceae-Asclepiadoideae deceptive flowers also occur, especially

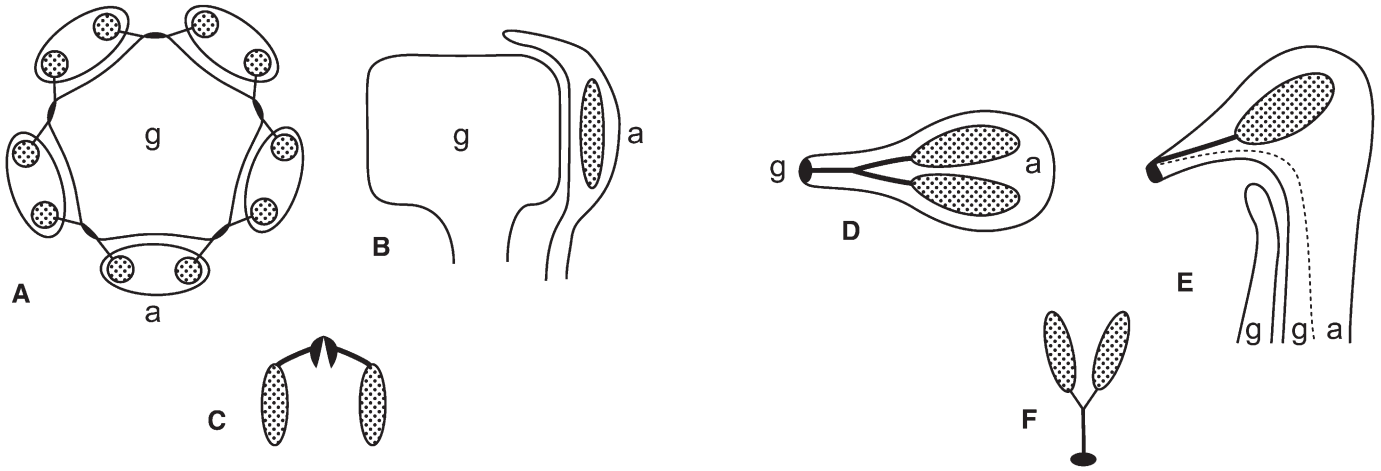

Fig. 9. Pollinarium formation by intimate synorganization of androecium and gynoecium. Pollinia are dotted. (A–C) Apocynaceae. (A) Transverse section of gynostegium. (B) Median longitudinal section of gynostegium. (C) Pollinarium with two pollinia and translator with clip (black). (D–F) Orchidaceae. (D) Transverse section of gynostemium. (E) Median longitudinal section of gynostemium. Dotted line indicates the virtual borderline between the congenitally fused androecium and gynoecium. (F) Pollinarium with two pollinia and translator with glue (black). a, androecium; g, gynoecium.

in in the highly diverse Ceropegieae (Jürgens et al., 2006) but are less intensively studied than in orchids, and pollinator specificity is less conspicous in asclepiads (Wyatt and Lipow, 2007). Pollen dispersal units are diverse in both Orchidaceae (Pacini, 2008) and asclepiads (Dannenbaum and Schill, 1991). In both cases, formation of the translator with the glue or clip evolved from the upper part of the stigmatic region by transfunctionalization and by restriction of the functional stigma to a lower part of the former stigma. An extreme gynostemium is also present in *Aristolochia* (Aristolochiaceae) (Igersheim and Endress, 1998; González and Stevenson, 2000) and Stylidiaceae (Erbar, 1992) but in both without evolution of pollinaria.

NECTARIES

Floral nectaries are widespread and diverse in angiosperms morphologically and histologically (Vogel, 1977; Fahn, 1979; Pacini et al., 2003; Bernardello, 2007). In basal angiosperms, nectaries are located on various floral organs, such as tepals, stamens, or carpels, and they are not elaborate (see Endress, 2010c). In monocots, septal nectaries (on the carpel flanks) are most prominent (Daumann, 1970; Vogel, 1981; Smets et al., 2000; Rudall, 2002a); they occur in no other subclade of angiosperms. The nectariferous region at the carpel flanks mostly becomes hidden developmentally by differential postgenital or congenital fusion of the carpels (Hartl and Severin, 1981; van Heel, 1988; Remizowa et al., 2008). Such internalized secretory surfaces are well protected, and they became greatly increased in several groups to form labyrinthine nectaries (Vogel, 1977), such as in some Arecaceae (Stauffer et al., 2009), Haemodoraceae (Simpson, 1993), and Bromeliaceae (Böhme, 1988). Such nectaries produce large amounts of nectar, and pollinators are often large animals, such as birds, bats, or primates. More rarely in monocots, nectaries are on tepals (Pandanales, Orchidaceae in Asparagales, Liliales; Endress, 1995) or other floral organs (part of Iridaceae in Asparagales, Rudall et al., 2003). In basal eudicots, nectaries are diverse, mostly located on petals (staminodes) or carpels (Erbar et al., 1999; Endress, 2010a). In core eudicots, the most important nectary innovation is the advent of disc nectaries in the area between androecium and gynoecium and sometimes also encompassing the area of the androecium; disc nectaries attained some independence from other floral organs. In addition, other forms have evolved repeatedly in various groups, e.g., hair nectaries in Malvales (Vogel, 1977, 1997, 2000) and Dipsacales (Wagenitz and Laing, 1984). In many angiosperm groups, nectaries were lost and other rewards became important, such as in pollen flowers (e.g., Dilleniaceae, Endress, 1997; many Commelinales, Vogel, 1981) or oil flowers (Vogel, 1974), or rewards became superfluous, such as in abiotically pollinated flowers (e.g., most Fagales and Poales), or nectaries became reinstated at new sites (Vogel, 1997).

EXTREME INCREASE OR REDUCTION IN SIZE

Increase and reduction of organ size are limited by morphogenetic and ecological constraints. Extreme forms are possible under special circumstances (Davis et al., 2008). For instance, the largest angiosperm flowers, which reach a meter in diameter in the parasitic *Rafflesia arnoldii*, sit on the ground (attached to the host), which provides support. In addition, presumably the unusually large cell size of their tissues provides an architecture that is not too heavy for self support. The longest flowers in the climber *Aristolochia grandiflora* hang on an elastic pedicel. Similarly, the large flowers of *Nymphaea* (Nymphaeaceae) are supported by the water surface, on which they are positioned. Also, the long necks in the flowers of some water plants are only possible because they are suspended in the water. The largest anthers reported in angiosperms, which occur in *Phenakospermum* (Strelitziaceae) and reach 7 cm length (Kress and Stone, 1993), rest in the closed perianth keel at anthesis, and are only exposed at the first visit by a pollinating bat. This extreme size would probably be difficult to maintain if the anthers were freely exposed before pollination.

In contrast, small sizes may be found in plants with underwater flowers. For instance, in *Najas* (Hydrocharitaceae), the ovary wall is only two cell layers thick (because the ovary is inferior, this structure even incorporates the floral base!) (Swamy and Lakshmanan, 1962), which is only possible because the ovary is supported by the water. Many water plants have reduced

flowers both in number of organs and in size because they have a constant water supply and need only a minimum of protective tissues. Examples are Hydatellaceae among basal angiosperms, the former Lemnaceae (now in Araceae) among monocots, and *Callitriche* in Plantaginaceae among eudicots).

PROGRESSIVE ELABORATIONS AND KEY INNOVATIONS VS.FIRST OCCURRENCE OF FEATURES IN PHYLOGENY

Newly evolved features may become key innovations and then characterize large clades. Often they are also sporadically present in other clades without being key innovations in those (Fig. 1). Some of the features discussed above may be such key innovations and are summarized in this section. When new features become fixed, flexibility may appear at other levels with new structures. Thus diversification appears at ever-new structural levels (Endress, 1987c, 1990, 1994a, 2006). (1) Pentamerous flowers are predominant in core eudicots but occur sporadically in Ranunculales and Sabiaceae and very few monocots. (2) Monosymmetric flowers are characteristic, among monocots for Orchidaceae and Zingiberales and among core eudicots for Fabales (Fabaceae, Polygalaceae), Lamiales, Dipsacales, and many Asterales, and they also occur occasionally in many other clades. (3) A perianth that is differentiated into sepals and petals is predominant in core eudicots and among monocots especially in Commelinales and Zingiberales. It occurs sporadically in, e.g., Alismatales and Ranunculales. (4) Sympetaly characterizes asterids, especially euasterids; it is sporadically present in monocots (e.g., some Burmanniaceae), basal eudicots (some Menispermaceae, *Consolida* in Ranunculaceae), and other core eudicots (e.g., Crassulaceae, Malvaceae). (5) Fusion of stamens and petals in the same sectors (stapet) is common in many monocots and dominates euasterids but also occurs in a few core Ranunculales and in Sabiaceae. (6) Haplostemony characterizes euasterids, but is also present in smaller clades, among monocots, e.g., in a few Alismatales, Burmanniaceae, Iridaceae, some Poales, and among eudicots, e.g., in Vitales, Santalales, and Celastrales. (7) A pollen sac placentoid is predominant in Lamiales but also occurs sporadically in some other lamiids and rarely in a few monocots (e.g., Orchidaceae, Costaceae). (8) Pollinaria are a key innovation in Orchidaceae and Apocynaceae and are otherwise not known. They require a stable floral organization with fixed number and position of floral organs, but a new level of diversity arises with novel appendages on the petal surface. (9) Syncarpy is a key innovation in core eudicots and monocots. It occurs sporadically in basal angiosperms (e.g., Nymphaeaceae, Annonaceae, Canellaceae, Piperacae, Aristolochiaceae) and basal eudicots (Papaveraceae, Sabiaceae, Trochodendraceae, Buxaceae). (10) A compitum (mostly intragynoecial or by postgenital fusion of the carpel tips) appears to be predominant in monocots and core eudicots (perhaps lacking in Dilleniaceae) and is most likely a key innovation in these groups. An extragynoecial compitum is present in a number of basal angiosperms (most pluricarpellate members of the ANITA grade, including *Amborella*, and several magnoliids) and basal eudicots (some core Ranunculales). (11) An inferior ovary characterizes among monocots, the Dioscoreales, Orchidaceae, and Zingiberales and among core eudicots, the Cucurbitales-Fagales clade, Santalales, Cornales, Rubiaceae, and campanulids. Minor occurrences are found in basal angiosperms, in Nymphaeaceae, Eupomatiaceae, Gomortegaceae, Hernandiaceae, Aristolochiaceae, in monocots, in some Alismatales. (12) Unitegmic ovules are a key innovation in asterids. They also occur sporadically in basal angiosperms (Ceratophyllaceae, Siparunaceae, Piperaceae, Hydnoraceae), very rarely in monocots (especially a few Alismatales) and, among eudicots, very rarely in Ranunculales, in Sabiaceae, in most Fagales and some other members of the nitrogen-fixing clades, and sporadically in some other orders. (13) Incompletely tenuinucellar ovules are a key innovation in asterids. They also characterize some larger clades of monocots, especially Dioscoreales, parts of Asparagales and Commelinales, and Poales, as well as some other eudicots, such part of the COM clade, and part of Brassicales). (14) Tenuinucellar ovules are a key innovation in Orchidaceae and Triuridaceae among monocots and in Gentianales, Lamiales, and Asterales among eudicots.

CHANGING EMPHASIS OF EVOLUTIONARY STABILITY AND LABILITY

Some features are relatively labile (evolutionarily flexible) in basal angiosperms and have been stabilized in the derived groups. Floral phyllotaxis is stabilized to whorled in monocots and core eudicots. Floral organ number is stabilized to 3-merous in monocots and 5-merous in core eudicots. Anther dehiscence is labile in basal angiosperms (simple longitudinal or flaps or H-shaped) because of often bulky stamens (Hufford and Endress, 1989) and became canalized to simple longitudinal in monocots and core eudicots. Integument thickness in basal angiosperms is labile (Endress and Igersheim, 2000a) and became more stable in monocots and core eudicots (Endress, 2010a). Ovule curvature is more variable in basal than in more derived angiosperms based on the more common occurrence of orthotropous ovules in addition to variously curved ones. Pseudocrassinucellar ovules have been recorded only from basal groups, such as Hydatellaceae (Rudall et al., 2008), Acorales (Rudall and Furness, 1997), Alismatales (Alismataceae p.p., True Araceae p.p., Hydrocharitacae p.p., Limnocharitaceae, p.p., Zosteraceae; Igersheim et al., 2001), and Ranunculales (Papaveraceae, Ranunculaceae; Endress and Igersheim, 1999).

Other features are relatively uniform in basal angiosperms and become more diverse (and flexible) in derived groups. Flowers in basal angiosperms are polysymmetric (except for sporadic monosymmetry by reduction; Endress, 1999, 2001a), whereas monosymmetry and asymmetry characterize derived clades, while polysymmetry is also retained. Flowers in basal angiosperms have largely unfused organs, whereas the potential of fusion and nonfusion of organs provides more evolutionary flexibility in derived clades, and especially fusion of petals enables the easy formation of a diversity of floral shapes used for various floral biological syndromes. Thus syndromes in pollination biology are less diverse in early angiosperms, e.g., pollination by birds, bats, and other mammals is lacking (Endress, 2010c). Likewise, heteranthery is lacking, and the gamut of flower colors is restricted: red and blue flowers are largely lacking in basal angiosperms. Bisexual flowers are exclusively protogynous in basal angiosperms, but both protogynous and protandrous groups characterize derived groups (Endress, 2010c).

OUTLOOK

It may be expected that each newly originated feature is favorable under certain ecological circumstances and may survive

in certain clades, but only in rare cases will an innovation become a key innovation leading to strong diversification of a clade. Certain innovations appear to have originated many times, such as floral monosymmetry or petals. The continuing question is in what respects such innovations are homologous. If the same genetic networks are used for each separate origin, when and how did these networks evolve?

Why are some traits so conservative, such as the thecal anther organization, ovule organization, to some extent the carpel organization, or the perianth organ number in higher monocots, and why are other traits highly flexible? Why do floral structures go wild in families of parasitic plants that are not related to each other, especially in their weird androecium and gynoecium structure, and with extremes in size, when the giant flowers of *Rafflesia* and the dwarf female flowers of *Balanophora* are compared?

Floral characteristics of some of the only recently recognized larger clades (orders or supraordinal clades) are practically unknown, and those of many established groups (families) are only rudimentarily known. Thus, we know features of how families can be recognized. However, we know very little of how different features are (functionally) connected with each other during the development of flowers (e.g., features of morphology, anatomy, histology, embryology, pollination, and dispersal biology) because they are mostly not studied in concert. Our floral morphological concepts need to be continuously revised and improved. Likewise, integrating microevolutionary studies of smaller clades with angiosperm-wide macroevolutionary studies is a continuous task for the future (Friedman et al., 2008).

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